

FIGURE 1. A, B, C. *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland, 1948.—A. Leaves in lateral view (arrow) appear aciculate.—B. Leaves in abaxial view appear flattened and laminate.—C. Leaves in transverse section (arrows) exhibit slightly convex adaxial surfaces and more strongly convex abaxial surfaces.—D. Unidentified lycopsid in which the leaves appear to be acicular with very broad bases (arrow) or laminate; both conditions due to mode of preservation and position in the enclosing matrix. A, USNM 446319; B, USNM 446320; C, USNM 42686; D, USNM 446321.

theca Edwards, 1970 is an example of (1); *Cooksonia* Lang, 1937 (Edwards, 1970; Edwards & Feehan, 1980) is an example of (2); *Zosterophyllum* Penhallow, 1892 is an example of (3); and *Baragwanathia* is an example of (4). Other genera extant during the Late Silurian–Early Devonian with terminal, fusiform, indehiscent sporangia but without proven vascular tissue include *Salopella* Edwards & Richardson, 1974; *Hedeia* Cookson, 1935; and *Tortilicaulis* (?bryophyte) Ed-

wards, 1979. The earliest *Cooksonia*-like sporangia from Wenlock strata (end of the late Early Silurian, see Table 1) in Ireland (Edwards & Feehan, 1980; Edwards et al., 1983) are borne on axes in which the presence of vascular tissue has not been proven. Reniform sporangia with distal dehiscence, borne laterally on axes without proven vascular structures and referred to the zosterophylls (*Zosterophyllophytina*, Banks, 1975) are reported in association with *Baragwanathia* in a

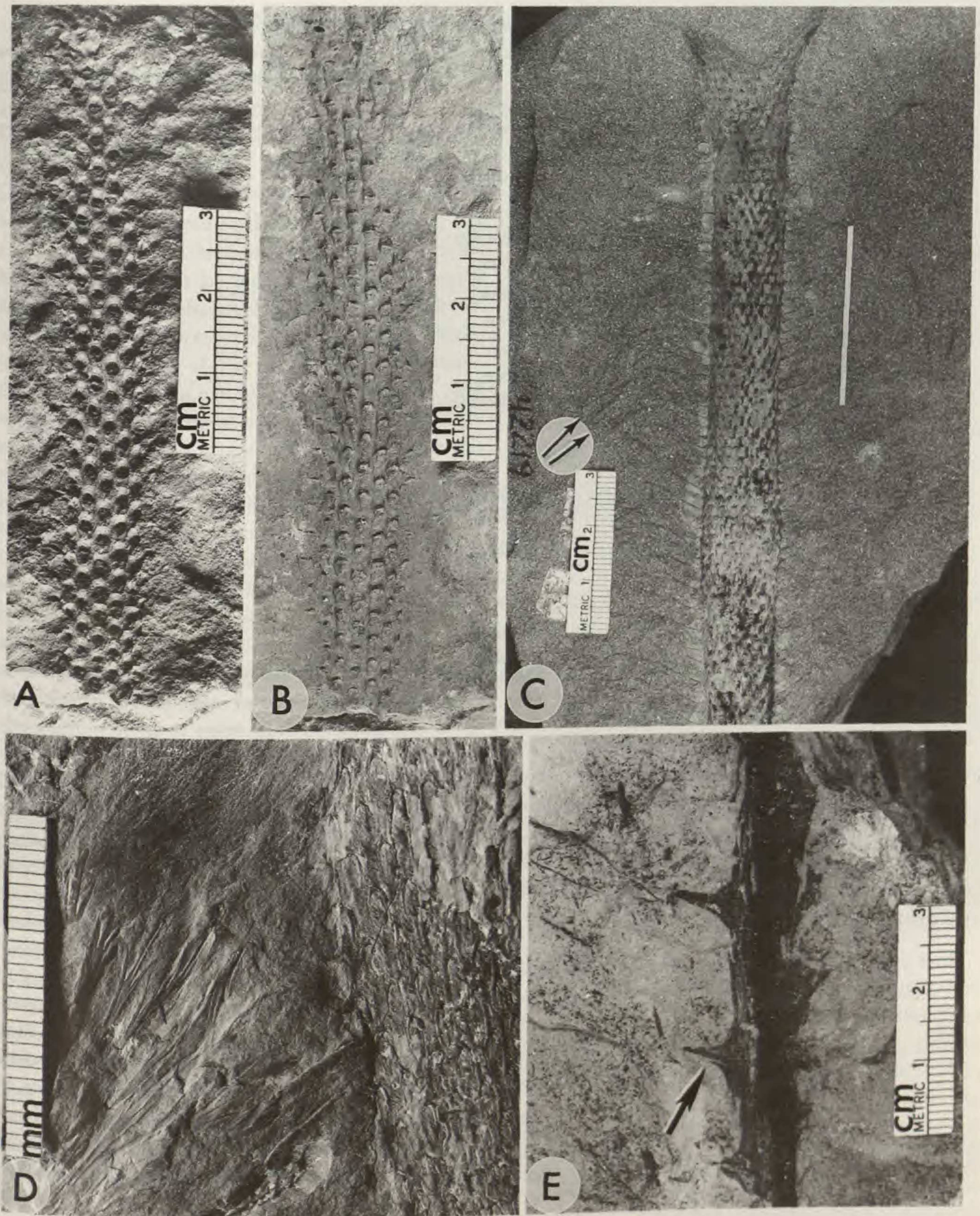


FIGURE 2. A, B. ?*Archaeosigillaria*. The lighting of specimens for photography can affect the interpretation of morphology and anatomy of decorticated lycopoid axes.—A. Specimen photographed with light source at a low angle from upper left.—B. Same specimen with light source at a low angle from the lower left. Inversion of the illustrations will exhibit the reverse effects. USNM 42217. C, D. *Colpodexylon trifurcatum* Banks, 1944.—C. Specimen exhibits the reverse effects. USNM 42219.—D. Trifurcation of the leaves clearly visible in well preserved specimen, NYSM 5240.—E. Axis with vascularized appendage (arrow) but lacking in sufficient other characteristics to allow classification with the lycopoids. USNM 422673.

TABLE 1. Silurian and Devonian time scale. Extracted from Harland et al. (1989).

Period	Epoch	Stage	Duration of intervals in millions of years			
			Began	Stage	Epoch	Period
CARBONIFEROUS						
	C ₁	Tournasian	362.5			
DEVONIAN						
Late	D ₃	Famennian	367.0	4.5	14.9	46.0
		Frasnian	377.4	10.4		
Middle	D ₂	Givetian	380.8	3.4	8.6	
		Eifelian	386.0	5.2		
Early	D ₁	Emsian	390.4	4.4	22.5	
		Pragian	396.3	5.9		
		Lochkovian	408.5	12.2		
SILURIAN						
Late	S ₄ Pridolian		410.7	2.2	15.5	30.5
	S ₃ Ludlovian	Ludfordian	415.1	4.4		
		Gorstian	424.0	8.9		
Early	S ₂ Wenlockian	Gleedonian	425.4	1.4	15.0	
		Whitwellian	426.1	0.7		
		Sherwoodian	430.4	4.3		
	S ₁ Llandoveryan	Telychian	432.6	2.2		
		Aeronian	436.9	4.3		
		Rhuddanian	439.0	2.1		

plant assemblage ostensibly of Gorstian age (early Late Silurian) (Tims & Chambers, 1984; Holmes, 1988).

SPORANGIA: ONTOGENY OF THE FUSIFORM, TERMINAL SPORANGIUM

Is it possible to define the sporangia of all of the early land plants as eusporangiate and/or leptosporangiate? We can only guess at the answer because of the paucity of evidence available. Bierhorst (1971: 266), in his discussion of filicalean sporangia, states:

An elongate sporangium, with longitudinal dehiscence, devoid of an annulus and terminally situated on an axial entity, is interpreted as the ancestral form of filicalean sporangia. This is essentially what is found in the Trimerophytaceae, which in our present state of knowledge may be ancestral to most all of the groups of ferns and fern-like plants (i.e., the Cladoxylales, the Aneurophytopsida, the coenopterid complex, the Ophioglossales and the Marattiales). It is further interpreted that the most primitive sporangium in this line had an ontogenetic history much like filicalean sporangia. That is, a single apical cell, which was also the apical cell of the axial entity upon which the sporangium was borne, ceased to produce lateral segments and divided periclinally. The outer cell produced the outer cell layer and possibly some of the cells of the inner wall layer. The inner cell produced sporogenous tissue, tapetum, and some or all of the cells of the inner wall. This would suggest that the tissue of the stalk, even if

contracted and distinct, was, in part, of the same origin and continuous with the outer tissues of the axis below. This is in contradiction to some previously published interpretations but seems to fit well all the old and recently acquired evidence.

I agree completely with this interpretation of the ontogeny of the sporangium as it could apply to some early vascular plants, but can the sporangium be defined as leptosporangiate or eusporangiate? Bierhorst (1971: 267) remarked that the terms "leptosporangium" and "eusporangium" should be abandoned as too vague and presenting false impressions of their taxonomic value. He did add, however, that the "leptosporangium" is considered the most primitive among most vascular plants. I agree with that conclusion and would interpret the above ontogeny of the terminal, fusiform sporangium in early land plants as a variation of the "leptosporangium." The terminal, fusiform sporangium, as thus far documented in the fossil record, is subtended by a vascular strand; this lends more credence to the interpretation of the ontogeny of the sporangium as a modified extension of the growth of the stem apex. However, with the production of the sporangium, growth of the stem ceased, and additional vegetative growth would have required continuous branching and spreading of a rhizome or other vegetatively active portions of the plant.

A line of dehiscence was lacking in the sporangia of the Silurian vascular plants that bore elongate, fusiform sporangia. The structure appeared later in the Pragian (middle Early Devonian), if, as an example, its presence may be interpreted from the specimen of *Dawsonites subarcuatus* Tims & Chambers, 1984. The terminal sporangium with a well-developed, longitudinal line of dehiscence became particularly evident among the trimerophytes in the Emsian (upper Lower Devonian) as is clearly demonstrated in *Psilophyton dawsonii* Banks et al., 1975. In *P. dawsonii*, the outermost, thickened cortical cells of the ultimate, dichotomous divisions of the axis are continuous with the wall of the sporangium. A line of dehiscence, an "annulus," is formed as a result of a reduction in the thickening of the anticlinal and periclinal walls of two contiguous rows of cells that extend along the length of the sporangium on the inner side relative to the dichotomy of the shoot. A transverse section of a permineralized pair of such sporangia has the appearance of two letters C, one normally positioned, the other reversed, the opening in the body of the letters representing the line of dehiscence. The line of dehiscence in the terminal, fusiform sporangium arose at some time between late Wenlockian (Early Silurian) and the Pragian (middle Early Devonian), but fossil evidence that could bridge the gap is lacking. The morphology and probably the ontogeny of the terminal, fusiform, longitudinally dehiscent sporangium continue to be recognizable throughout the Devonian. The sporangium of this form is characteristic of the trimerophytes (Trimerophytina Banks, 1975) and progymnosperms (Progymnospermopsida Beck, 1960) in such genera as *Psilophyton* Dawson, 1859; *Rellimia* Leclercq & Bonamo, 1973; *Tetraxylopteris* Beck, 1957, and even *Archaeopteris* Dawson, 1871. Bierhorst's (1971) interpretation of the ontogeny of fusiform sporangia can serve as the starting point for detailed study of fossils of such sporangia. Specimens of fossil material are available that probably could provide significant ontogenetic detail if new and innovative laboratory techniques were applied to their study. The significance of such studies can only corroborate Bierhorst's interpretation and help establish the origins of what may be termed a form of the "leptosporangium."

SPORANGIA: ONTOGENY OF THE RENIFORM, TERMINAL SPORANGIUM

Interpretation of the probable ontogeny of the terminal, fusiform sporangium stimulates formulation of a hypothesis on the ontogeny of the terminal, globular or reniform sporangium as seen in

late Middle Silurian and Early Devonian genera. The size and morphology of the sporangia leads to the hypothesis that the apical meristem of the subtending axes in these fossil plants comprised more than the single apical initial that has been suggested for the plants with terminal, fusiform sporangia. There may, instead, have been several apical initials that would have led to the formation of a morphologically distinct and more robust sporangium. Such a cluster of apical initials could serve as the basis in the definition of the ontogeny of a "eusporangium" as:

... a group of cells, superficial in position, [that] by periclinal division forms inner and outer cells, the inner forming sporogenous cells, the outer sterile cells only. . . . The outer layer, the *primary wall cells*, by divisions both periclinal and anticlinal forms the wall, a layer of tissue when mature about three cells thick. The inner layer, the *primary sporogenous cells*, by divisions in various planes, forms a large number of *spore mother cells* or *sporocytes* (Eames, 1936: 8).

In the fossils, the wall of the sporangium is continuous with the axis that supports it, whether that axis is the main axis or a lateral shoot, and, accordingly, the sporangium lacks what may be termed a stalk. In both the reniform and fusiform sporangia, among the fossils at hand, the vascular strand of the main axis or of a lateral shoot extends into the base of the sporangium. The sporangium forms the terminus of the axis or shoot, and the formation of the sporangium depletes the apical meristem. Subsequent growth of the plant would have relied upon the rapid and steady growth and spread of the vegetative portions of the plant if such were present.

A mechanism for distal dehiscence of terminal, reniform sporangia was evident in the late Early Devonian (Dittonian Stage correlative in part to the Late Lochkovian) species *Cooksonia caledonica* Edwards, 1970. This mechanism and its position on the sporangium were also characteristic of the zosterophylls, which were represented in the ostensibly Gorstian age flora in Australia. The zosterophylls continued well up into the Devonian (Hueber & Grierson, 1961; Hueber & Banks, 1979) with a variety of morphologies and ornamentations to the axes, but at the same time the form of the sporangium was retained throughout their history. The only variation seen in the sporangium is a shifting of the line of dehiscence from distal and complete (most genera) to lateral and complete (e.g., *Crenaticaulis verruculosus* Banks & Davis, 1969). This shift of position resulted in a morphological change in the symmetry of the sporangia from equal valved (common) to unequal valved (rare). In the zosterophylls the sporangia are usu-

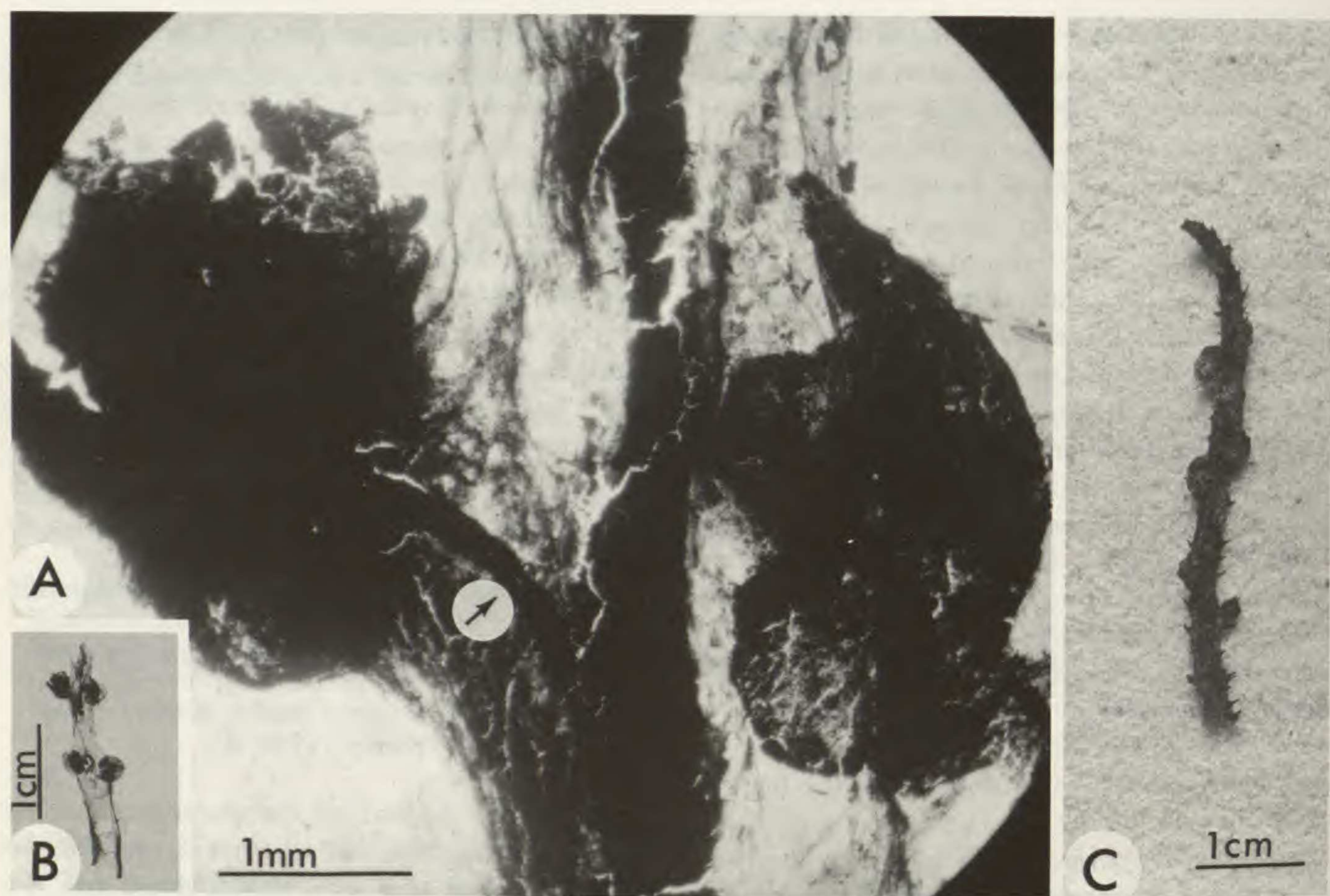


FIGURE 3. A, C. Fertile and vegetative axes of *Sawdonia ornata* (Dawson) Hueber.—A. Sporangium, as seen on upper left in B, with subtending vascular strand (arrow).—B. Portion of fertile axis, naturally retted, with subopposite sporangia.—C. Vegetative axis, isolated from matrix, with lateral buds producing the illusion of sporangia as seen in B. A, B, Geological Survey of Canada Locality 6436; C, USNM 446310.

ally described as stalked and when well preserved exhibit a vascular trace to the base of the sporangium (Fig. 3A), suggesting that the sporangia terminate a lateral, fertile shoot (Fig. 3B). There also are instances, as in specimens of *Sawdonia ornata* (Dawson) Hueber, 1971, in which a specimen of such a zosterophyll seems, at first sight, to have sporangia arranged in files along the sides of the stem. However, when the specimen is isolated by maceration of the matrix, it is found that the supposed sporangia are undeveloped or dormant lateral buds (Fig. 3C). From these few facts it is possible to review an additional line of conjecture regarding the variation in morphology of the several genera in the Zosterophyllophytina.

SPORANGIA: THE ZOSTEROPHYLLS

The zosterophylls (Zosterophyllophytina) represented a group of plants whose origins were with cooksonioid plants characterized by terminal, globular to reniform sporangia. The plants characterized by terminal, fusiform sporangia and of the same relative age as the cooksonioids represented the basis for a wholly different lineage of early land plants.

The sporangia of the cooksonioids were probably derived from the apical initials of the aerial axes, and the production of the sporangia depleted the apical initials. If the arrangement of the sporangia in the zosterophylls was a product of the loss of the apical initials of (1) the central axis, (2) the earlier formed lateral axes with subsequent atrophy of the apex of the central axis, or (3) the lateral axes only, but in combination with the continued vigorous growth of the central apex, the possibility of describing the variation of morphology of members of the group may be developed (Niklas & Banks, 1990; Gerrienne, 1988; Gensel, 1982). I repeat that a cooksonioid plant could be the progenitor of the zosterophylls and that *Renalia* Gensel, 1976, could possibly represent a zosterophyll as suggested by Niklas & Banks (1990). Interestingly, the plant now known as *Renalia* was the plant that I referred to as *Cooksonia* (Hueber, 1964) when I first began reviewing the flora of the Gaspé Sandstone. The morphology of *Renalia* resembles that of *Cooksonia hemisphaerica* Lang, 1937, as seen in the restoration of the species by Ananiev & Stepanov (1969).

My intent here is to review the interpretations of the morphology of a few of the genera repre-

sented in the Zosterophyllophytina in light of the interpretations stated above. If *Renalia* is a zosterophyll, then it clearly reflects the ancestral form of the group in which the large, reniform, distally dehiscent sporangia have been derived from apical initials and the initials have been depleted on every segment of the aerial shoots (e.g., restoration by Gensel, 1976). Additional growth of the plant would depend on rapid spreading and growth of the basal or rhizomatose regions, if such were present; otherwise the whole plant was spent in the reproductive process.

Among the genera of zosterophylls I have observed in which the sporangia are borne in compact or lax spikes, the apex of the axis is present but quite small and perhaps was abortive; examples include *Rebuchia* (Dorf) Hueber, 1972; *Zosterophyllum australianum* Lang & Cookson, 1930; and *Z. myretonianum* Penhallow, 1892. I agree with Niklas & Banks (1990) and interpret these forms as ones in which growth of each, very short, lateral shoot rather rhythmically produced by the apical meristem ended with the production of a sporangium. The development of the sporangium exhausted the apical initials of the lateral shoots. Physiological pressures may have caused the apical meristem of the main axis to cease functioning after the production of the sporangia and spores. Replacement of the heavily depleted nutrients into the system was probably controlled by the volume and development of the vegetative portions of the plant. There is also the possibility that the growth was genetically controlled, and the plant was simply determinate.

Examples of the remaining forms I will review from category 3 above are those in which the apical initials of the short, lateral branches are depleted in the production of sporangia but in which the apical meristem of the main shoot continues vigorous growth. The genera in this grouping, with which I am better acquainted through observations at collecting sites, were perhaps the most active in vegetative growth among the zosterophylls. *Sawdonia*, for example, is found as masses of intermeshing stems; however, among hundreds of stems, only one bearing sporangia might be found. Such was also the case with *Serrulacaulis* Hueber & Banks, 1979, and to a lesser degree with *Crenaticaulis*. The sporangia in these genera are borne on short, lateral "stalks," and each was supplied with a vascular trace from the central vascular strand. Their arrangement was alternate to opposite, and they formed what may be termed a fertile region along the axis. Vegetative growth beyond the fertile region generally was extensive and was

terminated by a circinnate apex. One can only suggest that the large and very active vegetative growth was required to attain a concentration of auxins and nutrients that would stimulate and support reproductive activity in the stem apex. This group also had highly varied ornamentation of the stems. Some bore structures that apparently arose randomly from the protoderm and spanned the range of definition from trichome to emergence. In some genera, e.g., *Serrulacaulis* and *Crenaticaulis*, there appears to have been some influence from the apical meristem that governed an arrangement of the emergences into one or two orderly files along the margins of the stems. This characteristic may also have been influenced, at least in *Serrulacaulis*, by the morphology of the stems, which were apparently oval in cross section with the emergences borne along the opposing ridges. Any additional discussion of ornamentation requires supportive illustrative material and will have to be the subject of another paper.

The purpose in this review of sporangia and the speculations on their ontogenies in plants from the Silurian into the Devonian is so that I may express a heartfelt opinion. I do not agree with the hypothesis (Banks, 1968) that the zosterophylls are the progenitors of the lycopoids. I admit that a discussion of the ontogeny of the sporangium in the zosterophylls at this time, though sensible, is conjectural. If in the zosterophylls the apical meristem was depleted in the formation of the sporangium, I see that ontogeny of the sporangium as wholly different and separate from the ontogeny and resulting position of the sporangium in the lycopoids. The time-lapse slipping and sliding of telomic acrobatics hold little significance to me when one has evidence of the ontogeny, morphology, and anatomy of the sporangia in the Recent lycopoids as a key to the interpretation of evidence from the fossil record of the group.

SPORANGIA: INTERPRETING THE EARLY LYCOPSIDS

I suggested earlier here that the lycopoids were derived from cooksonioid stock principally on the basis of the morphology of the sporangium. My thoughts on the ontogeny of the sporangium in the zosterophylls relied upon the total activity and depletion of the apical meristem of the axis bearing the sporangium. To derive the lycopoid lineage from a stock of cooksonioid plants we need to hypothesize on what might have been the change in the growth activity of the apical meristem in the axes of the plant serving as the base stock. The suggestion was made here that the apical meristem

of those plants with terminal, globose or reniform sporangia comprised several apical initial cells. That apical meristem functioned in the formation of the body of the plant, the branching of the axis, and ultimately the formation of the sporangium. At some point in the 15-million-year period between late Homeric (late Middle Silurian) and Lochkovian (early Lower Devonian), a major evolutionary change in the activities of the apical meristem took place. The derivation of leaf primordia from cells at the side of the apical meristem would have been the first step toward the formation of the microphyllous leaf typifying the earliest Devonian lycopsid, *Drepanophycus* (Schweitzer, 1980). Sporangia would be derived from cells produced adjacent to the apical meristem in the same manner as the leaves in the early lycopsids. The "eusporangiate" form of the sporangia would be a genetically controlled feature carried over from the ancestral stock of cooksonioid plants.

What is the potential for interpreting the ontogeny of the sporangia in the remains of plants thought to represent the early lycopsids? In Recent lycopsids the primordium of a sporangium has three sites in which it may occur: (1) in the adaxial surface of a leaf primordium, (2) in the axil of a leaf primordium, or (3) in the protoderm of the stem immediately above the formation of a leaf primordium. In all of these instances the primordium for the sporangium arises from cells of the protoderm of a leaf or of the stem. The protoderm is a derivative of the apical initials and is produced continuously during the growth and expansion of the axis. The primordia of the leaves and sporangia are initiated secondarily and are very close to the early derivatives of the apical initials. They do not affect the activity of the apical initials except perhaps by the pressures they exert in the physically and perhaps genetically controlled development of the phyllotaxy. In the Recent lycopsids there is no vascular trace nor vestigial remains of procambial tissue entering the base of the sporangium. This characteristic could suggest that sporangia in the ancient lycopsids also were not supplied by vascular tissue. Such appears to be the case thus far among the early fossil lycopsids; none of the fertile material has been shown to have vascular tissue entering the "stalk" of the sporangium. The vein in the leaf remains only within close proximity of the base of the sporangium. *Asteroxylon mackiei* Kidston & Lang, 1920 (Lyon, 1964) is perhaps an exception to this observation. On this point I offer a hypothesis regarding the form and position of the sporangia in *A. mackiei*. I do not doubt the present interpretation so much as I would prefer to see

more serial sections in support of the reconstructed model by Joyce Collard prepared for a pamphlet for the Royal Scottish Museum in Edinburgh (Chaloner & MacDonald, 1980). Considering the fact that the sporangia are shown to exceed the length of the leaves, could the sporangium actually be borne adaxially on a leaf, perhaps some distance from the axil of the leaf? The extension of the leaf distally beyond the attachment of the sporangium might be quite short or nearly vestigial, as indicated in the reconstruction by the slight bulge in the distal valve of the sporangium. Location of the apex of a subtending sporophyll, if present, would require serial transverse or longitudinal sections from the point of attachment of the sporangial "stalk" through the full width of the sporangium. Median and near median longitudinal sections parallel to the long axis of the "stalk" would probably be the most instructive. Perhaps, also, well-prepared and closely monitored serial, longitudinal, thin-sections of the abundant and well-preserved remains of *Asteroxylon* will yield answers to the question of the ontogeny of the sporangium. In light of the position and morphology of the sporangium, one might hypothesize that the sporangium was initiated by a single or double row of several cells aligned transversely on the leaf primordium and not from the whole of the apical initials of the apex of a lateral shoot. If the presence and morphology of a sporophyll is demonstrated for *Asteroxylon*, it will probably be similar to that of *Kaulangiophyton*.

Kaulangiophyton acantha Gensel et al., 1969, is a species recently synonymized with *Drepanophycus spinaeformis* Göppert, 1852 (Rayner, 1984). Reexamination of the holotype and paratype specimens of *K. acantha* has resulted in the need to revise our interpretation of the morphology of the leaves and the relationship of the sporangia to the leaves. I demonstrate my reinterpretation of the species in Figure 4A and 4B with tracings of the photographs that were presented by Gensel et al. (1969: 271, figs. 5, 6). In Figure 5, a revised reconstruction of the species is presented. The leaves are 4–5 mm long, at least twice the length originally described. The sporangium was produced on the adaxial surface of the leaf, distally from the axis at a point about one-third the length of the leaf. The sporangia were large and exceeded the apex of the leaf. Most of the apices of the vegetative as well as fertile leaves were lost during the splitting of the matrix, but some remain, closely adpressed to the underside of the sporangium or plunging into the matrix below the point of attachment of the sporangium. As seen in side view, very fine

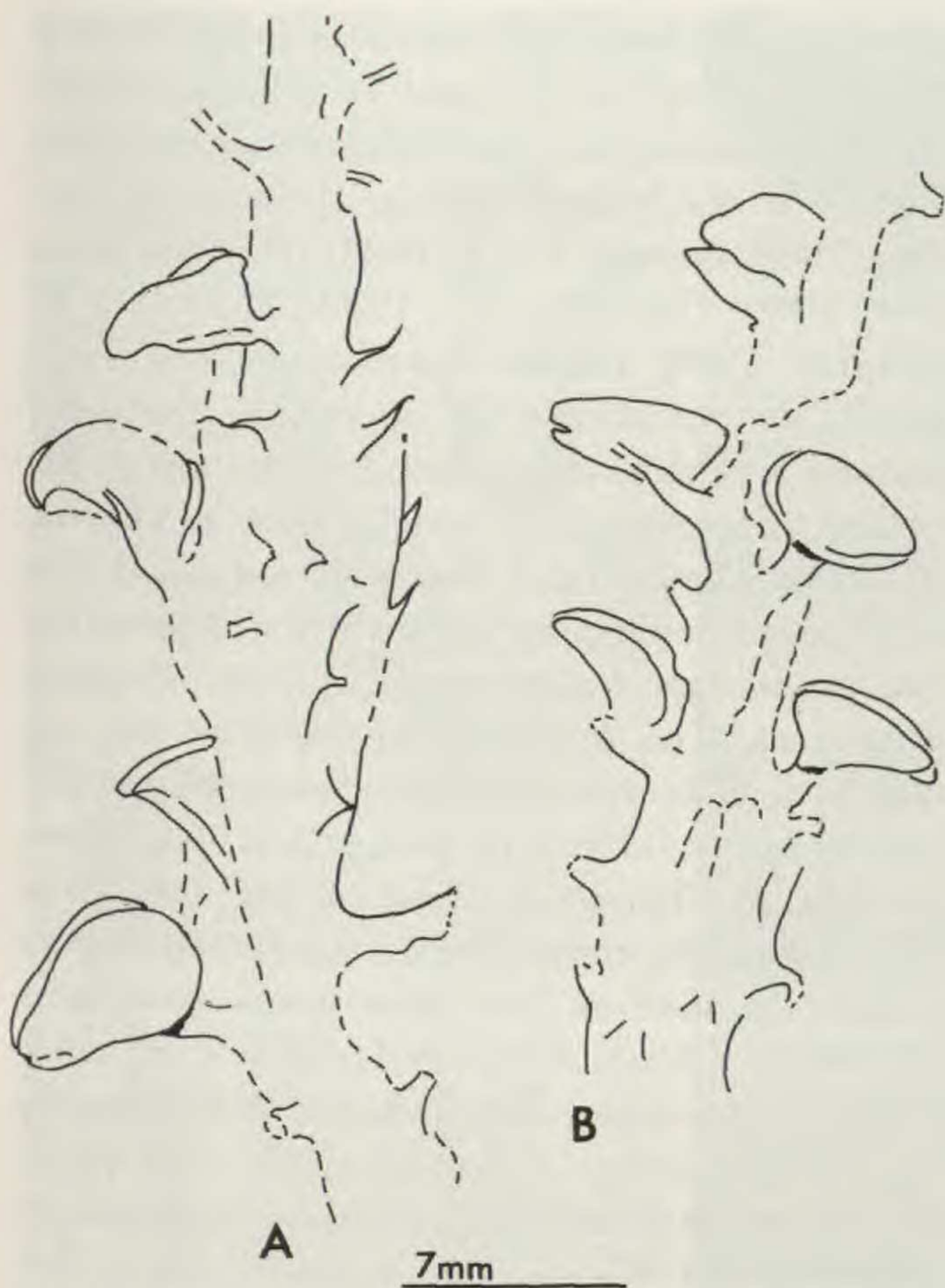


FIGURE 4. A, B. Tracings from photographs of *Kaulangiophyton akantha* Gensel, Kasper & Andrews, 1969.—A. Tracing of figure 5, page 271, Gensel et al. (1969), holotype, to emphasize details of morphology not clearly evident in the original photograph; USNM 43208.—B. Tracing of figure 6, page 271, Gensel et al., paratype, to emphasize details of morphology not clearly evident in the original photograph; USNM 43209.

lines of carbonized tissue extend outward into the matrix from the broad leaf bases and quite probably represent the vertically compressed body of the leaf. A well-defined line of dehiscence is present and is depicted in the tracings and in the revised reconstruction. The dehiscence is distal, equal, complete, and longitudinal to the axis of the subtending leaf. These findings relate *Kaulangiophyton* to the lycopsids and remove it as a hypothetical link to the zosterophylls. The sporangia were not borne on stalks but were instead borne on the adaxial surface of the leaves.

In *Asteroxylon*, the procambial cells in the body of the leaf (Fig. 6A, B) might have differentiated as xylary elements producing the vein observed in the "stalk" of the sporangium. Reproduction was probably initiated under the genetic and physiologic stimuli of auxin and nutrient accumulations in the stem apex. The evolution of the xylem and formation of the vein in the leaf might have resulted from the pressures exerted for the transport of nutrients required for the development of the spo-

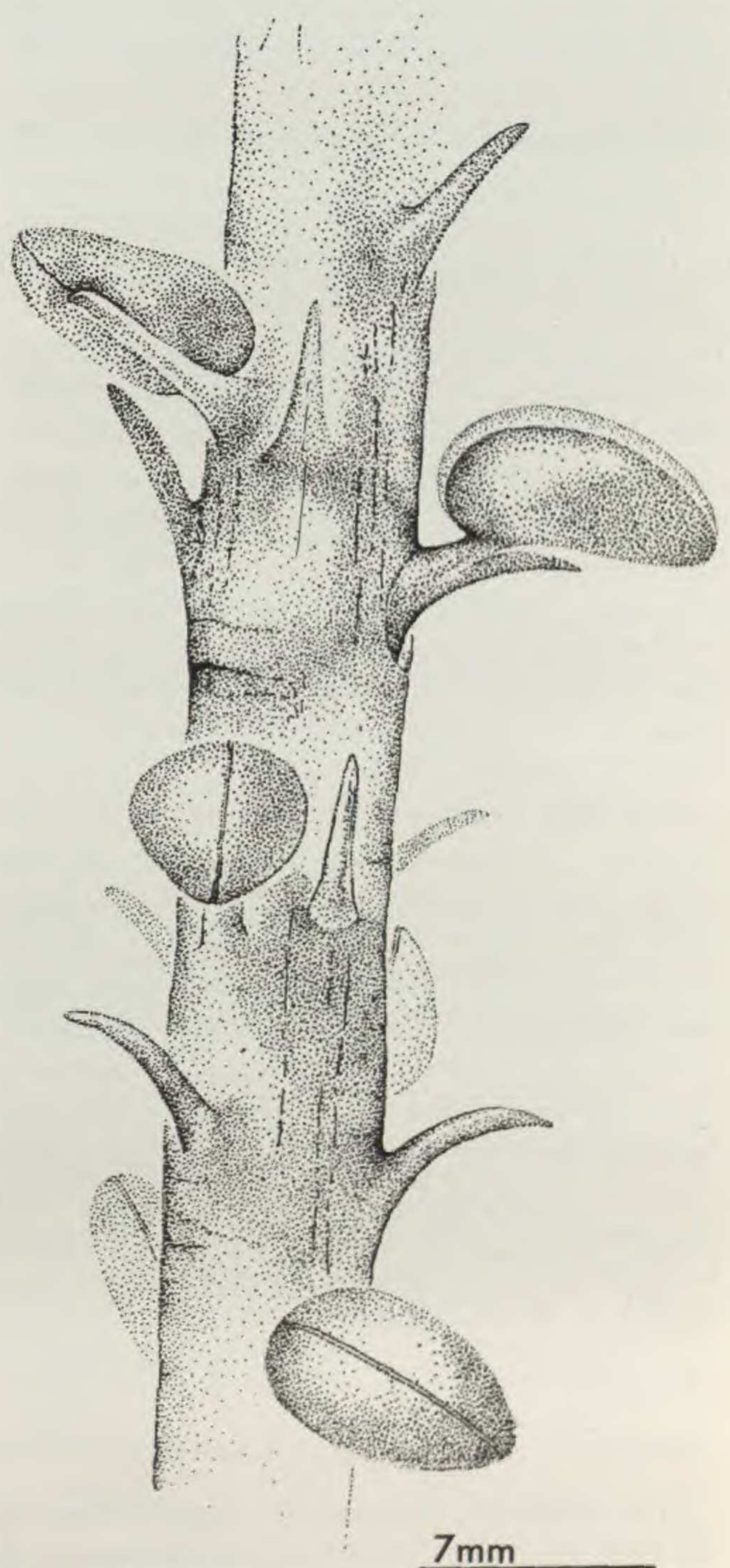


FIGURE 5. Reinterpreted restoration of the fertile zone in the species *Kaulangiophyton akantha* Gensel, Kasper & Andrews, 1969; figure 7, page 272.

rangium and spores. Transport of sufficient nutrients would have required a more efficient system than that of diffusion from the truncated vein as seen in vegetative leaves (Fig. 6C, D). Even more plausibly, one might suggest that leaves bearing sporangia, thus with two growth centers as opposed to sterile leaves with only one, produced higher levels of auxins causing more complete xylem differentiation regardless of the metabolic requirements of mature tissues on the water transport system.

THE APICAL MERISTEM OF *ASTEROXYLON*

A well-permineralized apical meristem of a Devonian lycopsid has not yet been illustrated to my knowledge. I thus illustrate here a median longitudinal section of a well-developed and very well preserved lateral branch of *Asteroxylon mackiei* (Fig. 7A–C). The ground-thin section was prepared by John Hutchison in 1952 from material given to Sergius H. Mamay by John Walton in 1951. The apex is flat and comprises remains of several apical initials (Fig. 7B.2), a region of central mother cells (Fig. 7B.4), zones of the partially delimited cortex (Fig. 7B.6), the regions of the procambium and differentiation of the xylem strand (Fig. 7B.7), a procambial strand leading to a leaf (Fig. 7B.5), leaf traces (Fig. 7B.8), leaf primordia (Fig. 7B.3), and leaves in various stages of growth (Fig. 7B.1). This fossilized apex resembles the morphology and anatomy of a Recent species of *Lycopodium*, *L. reflexum* Lamarck, as illustrated by a camera lucida drawing in Haupt (1953: 219). A paper by Wardlaw (1957) on the organization and reactivity of the shoot apex in vascular plants diagrammatically shows the apex of *Lycopodium* as flat. In the context of these illustrations one can appreciate more fully the significance of the morphology and anatomy of the apex of *Asteroxylon* and feel with more confidence that *Asteroxylon* is a bona fide lycopsid. The apex of a lateral branch on a specimen of *Drepanophycus gaspianus* in the form of a compression (Fig. 7D), suggests that the apical morphology in *Drepanophycus* may be the same as that in *Asteroxylon*.

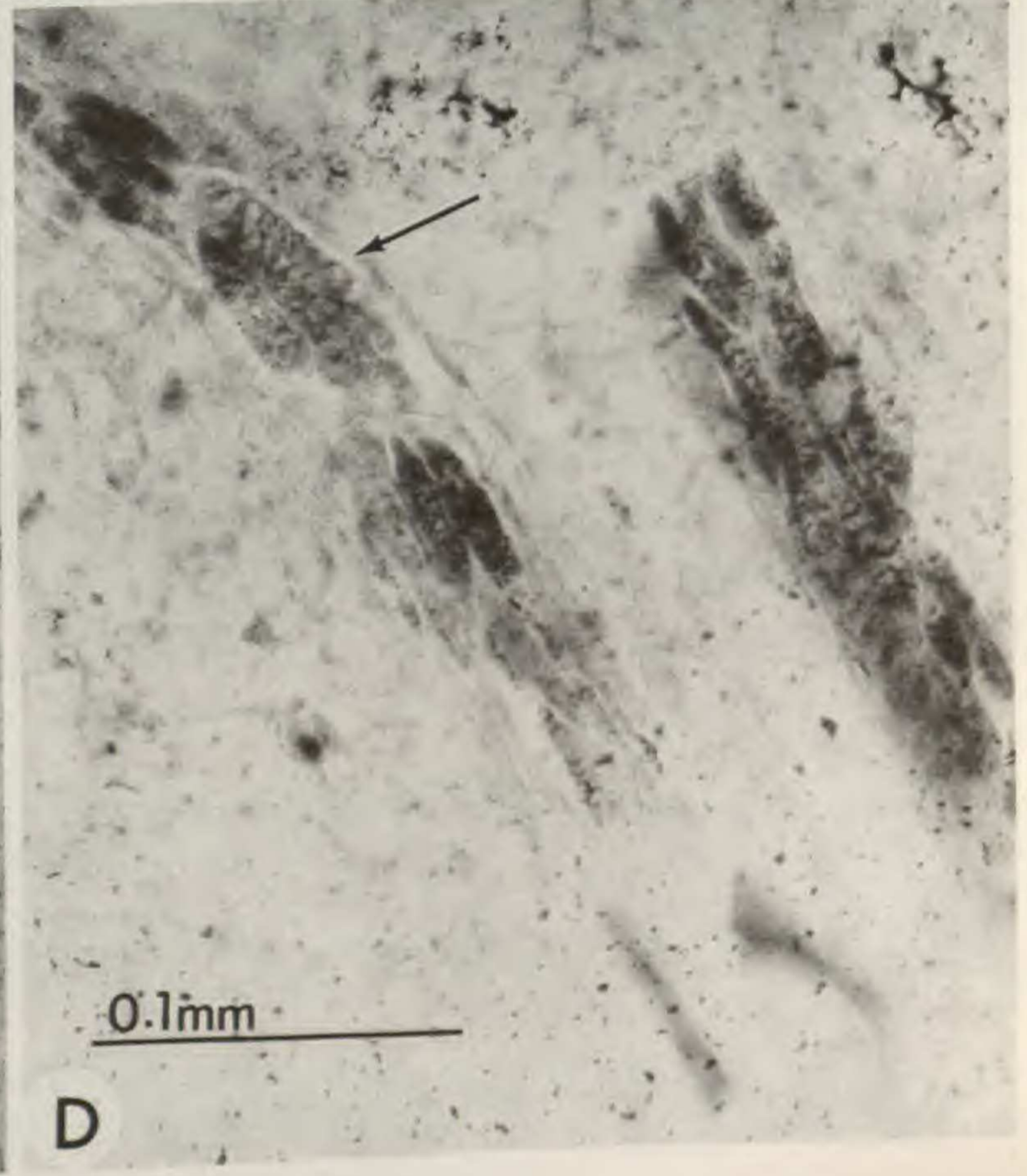
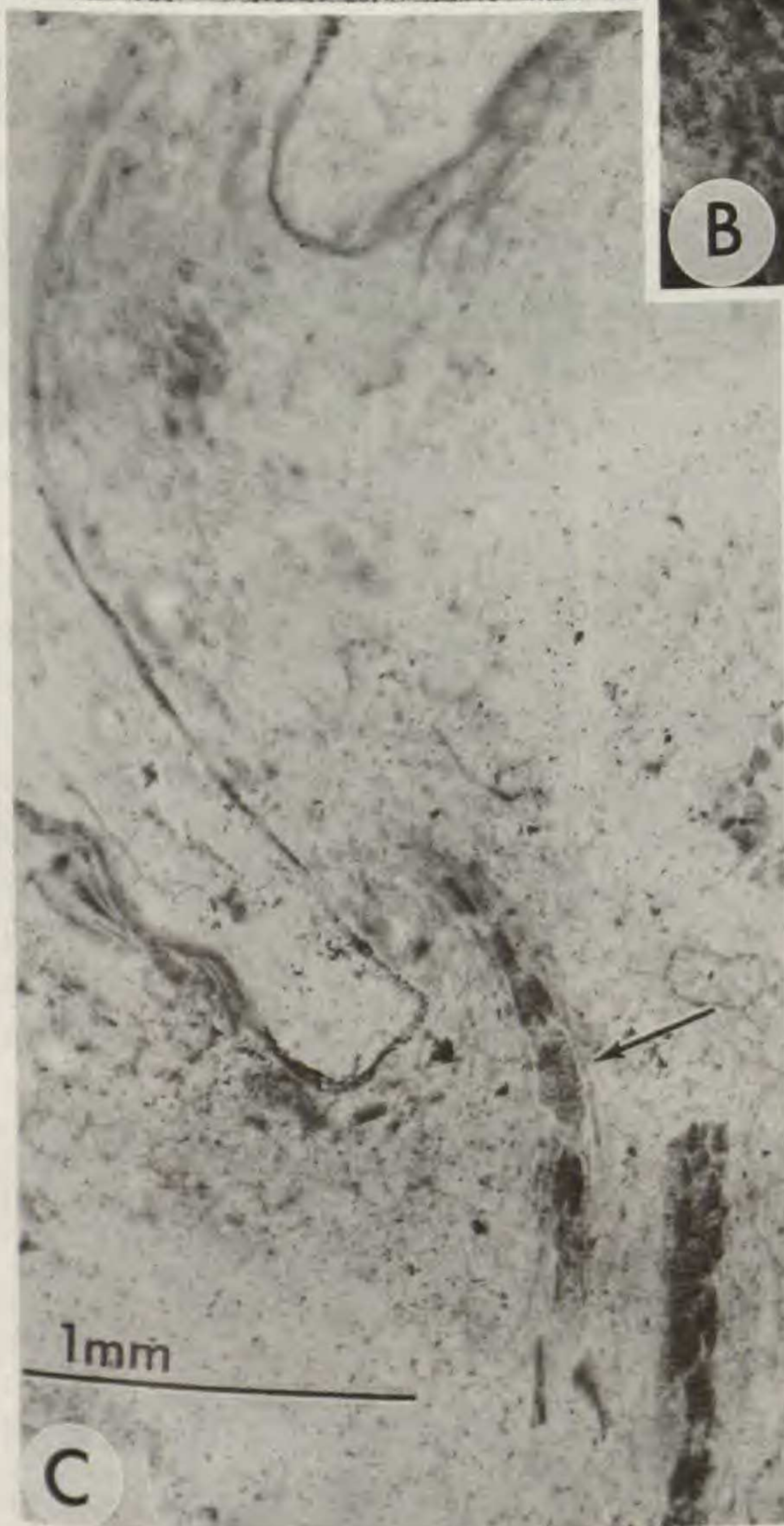
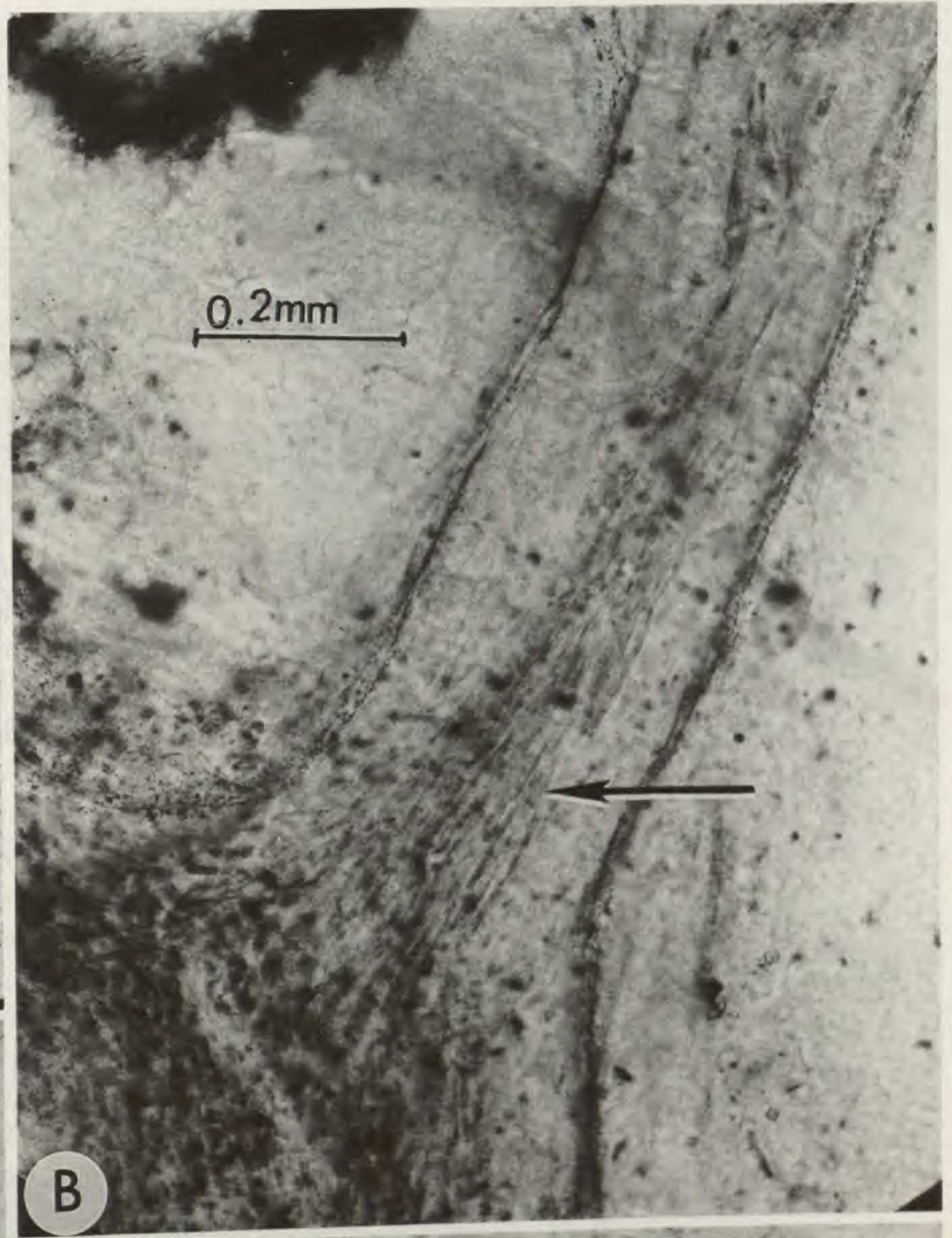
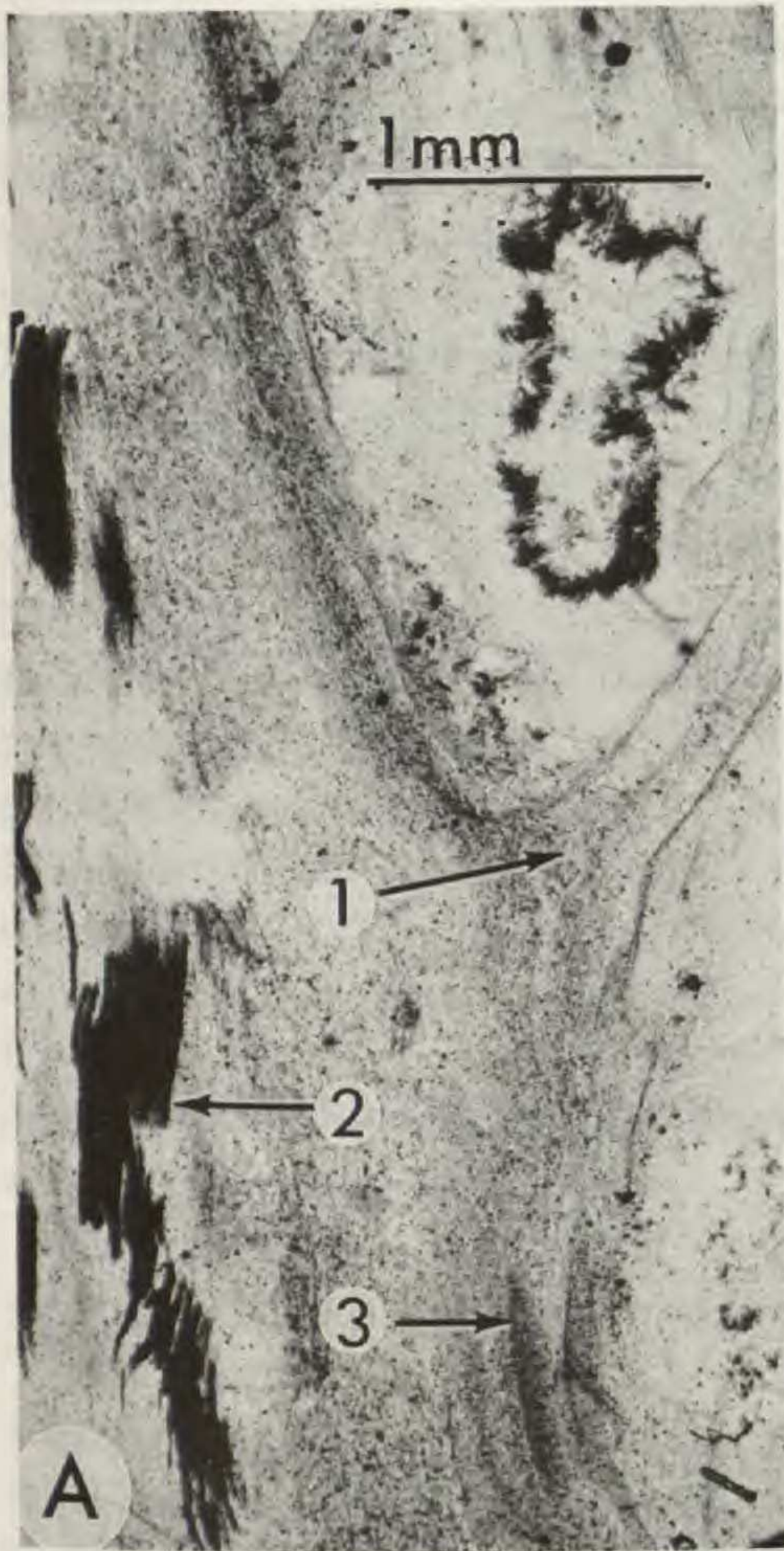
BARAGWANATHIA: ARGUABLY THE EARLIEST LYCOPSID

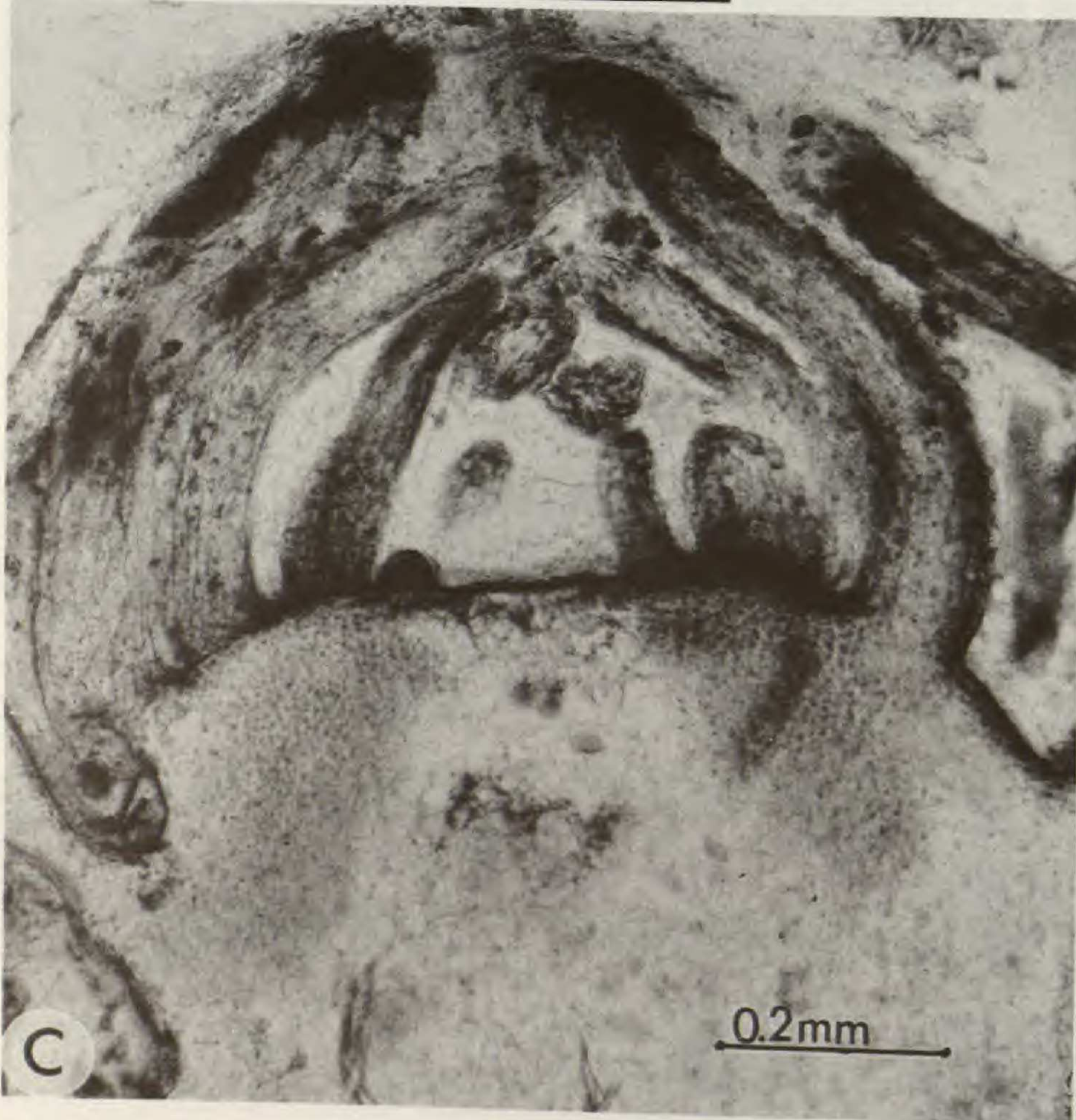
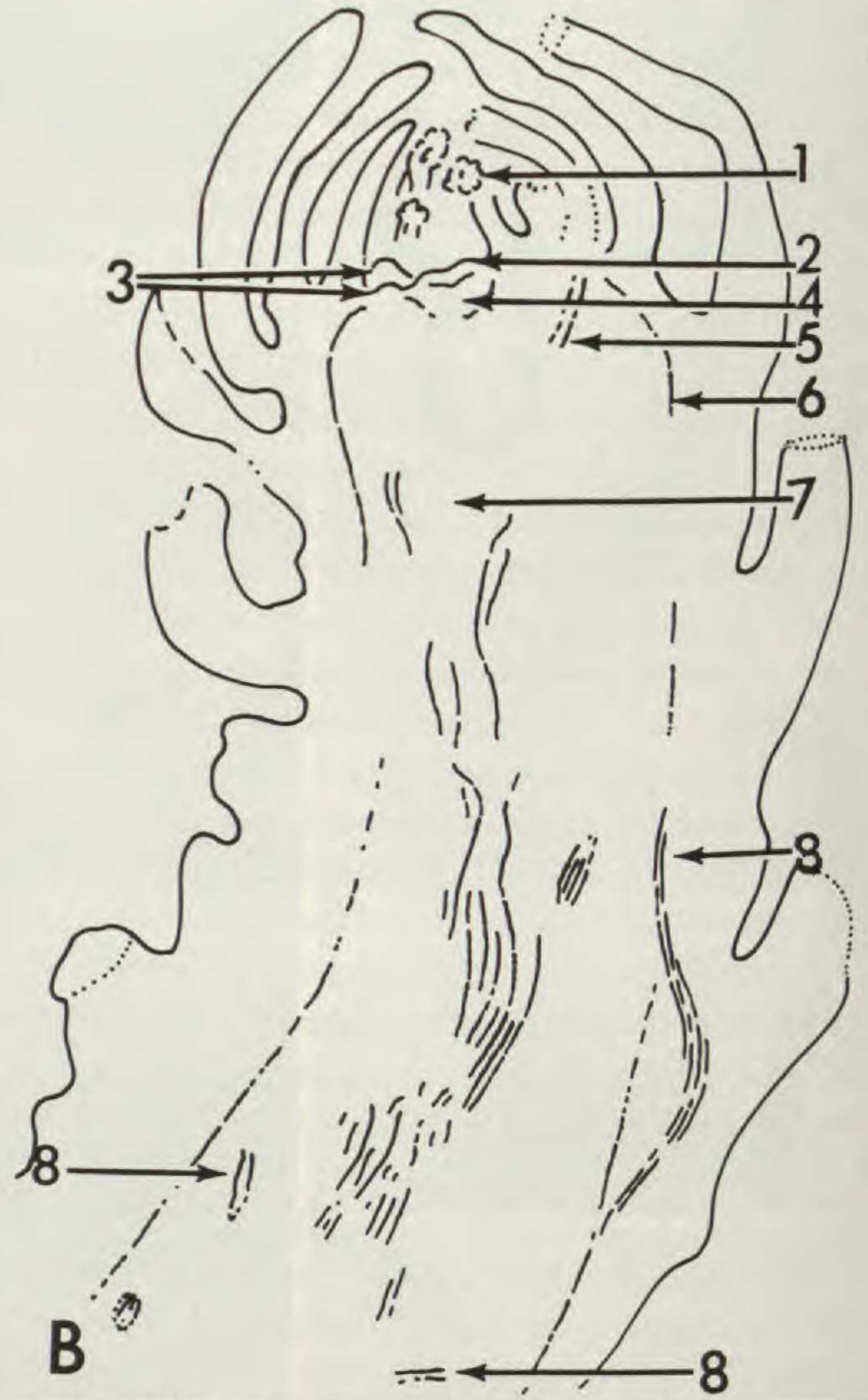
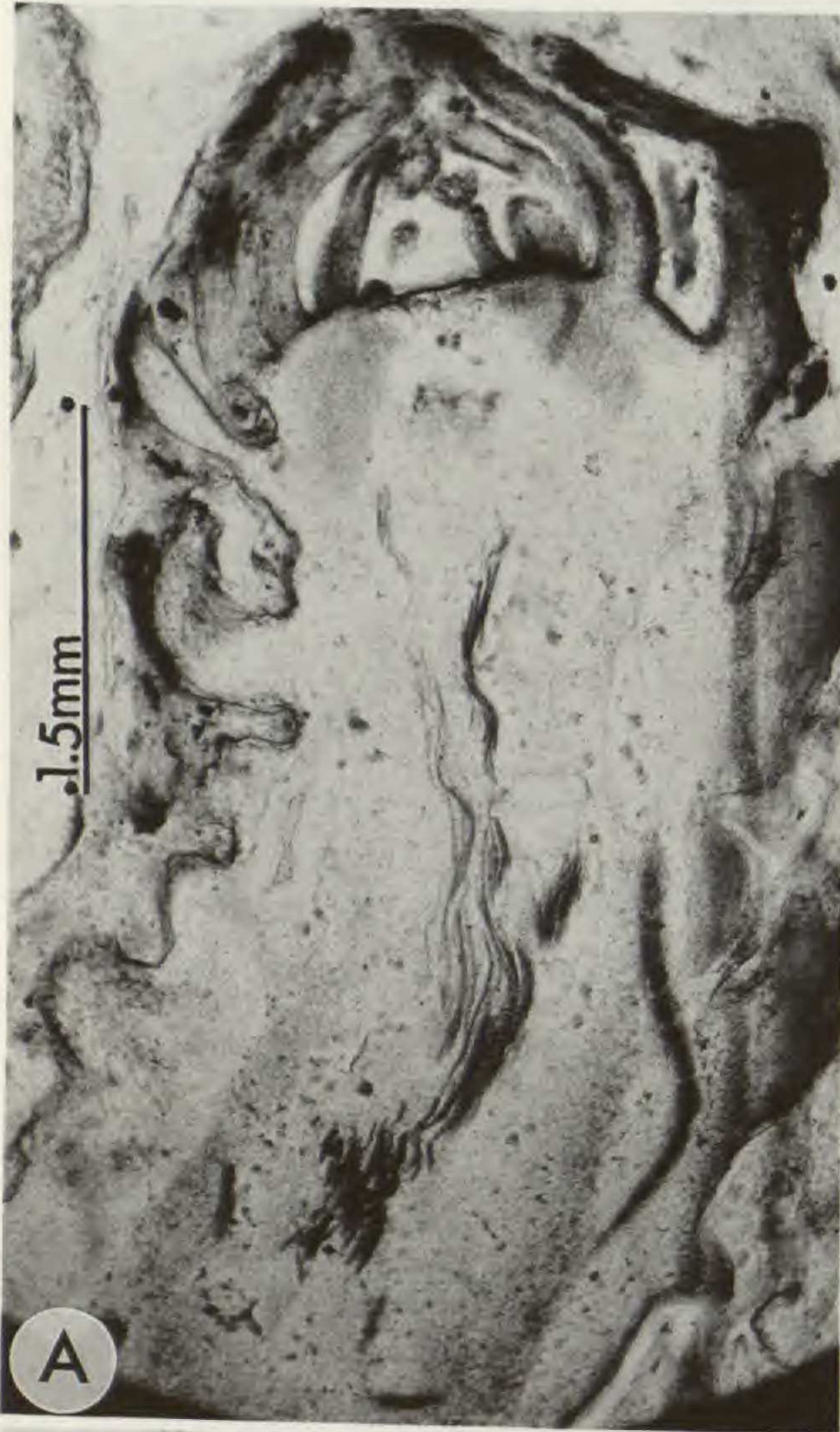
The lycopsids maintain the unique record for the longest continuously recognizable lineage of any vascular plant group, perhaps ranging from among the early land vascular plants of Gorstian age (lower Late Silurian) to the present, a period of nearly 424 million years (Table 1). However, the origin of the group is enigmatic and open to interpretation. No fossil has been found with a basic morphological or anatomical organization that could be

taken as a precursor to the species *Baragwanathia longifolia*, which is accepted by some paleobotanists, paleontologists, and geologists as the oldest member of the lycopsid lineage (Edwards & Fanning, 1985; Garratt, 1978, 1981; Garratt & Rickards, 1984; Garratt et al., 1984; Richardson & Edwards, 1989; Tims & Chambers, 1984). I personally do not accept the species as the oldest because I remain unconvinced of the age of the earliest stratigraphic occurrence of it in Victoria, Australia. The dating, I feel, is too subjective as it is not based on adequate numbers of well-preserved and (most importantly) unambiguously identified graptolites. Two localities are involved and are interpreted as approximately stratigraphically equivalent by Garratt & Rickards (1984). Their localities are Limestone Road (4) and Ghin Ghin (1), Victoria, Australia. The few specimens of graptolites identified as *Bohemograptus bohemicus bohemicus* (Barrande) from Locality 4 are illustrated by the authors and are used in defining the biostratigraphic age of the sediments. The species *B. bohemicus* is cited as a common, cosmopolitan graptolite not known from strata younger than Ludlow (Late Silurian; see Table 1). The specimen that was formerly identified by Garratt (1978, fig. 5A) as belonging to the *Pristiograptus dubius* (Suess) group is re-illustrated as *B. bohemicus bohemicus* (Barrande). The authors, however, give neither descriptions nor comparisons in support of the identification of the species and subspecies. They mention that one or two specimens in the collections show morphological variations from the species but that those particular specimens do not change the interpretation of the age of the site from Ludlow. If the confidence of identification is to the level of subspecies, it would seem appropriate to furnish a description that would fully justify the taxonomic position of the specimens at hand.

The identification of specimens of graptolites from Locality 1 is accompanied by a comparison to *Monograptus uncinatus* sens. str., a species restricted to the Gorstian (Lower Ludlow or lower Late Silurian). However, the authors (Garratt & Rickards, 1984) are not fully confident in their identification of the specimens and refer to them

FIGURE 6. A, B, C, D. Anatomy of leaves and veins of *Asteroxylon mackiei* Kidston & Lang, 1920. —A. Slightly oblique, longitudinal section of axis showing at (1) a leaf base with undifferentiated procambium extending downward toward the leaf trace and upward into the leaf, at (2) portions of the central xylem strand, and at (3) the leaf trace. —B. Enlarged view of the median longitudinal section of the leaf, as seen in A, with procambium extending into the center of the leaf. —C. Longitudinal section of leaf base with partially differentiated xylem of the vein (arrow). —D. Enlarged view of the partially differentiated tracheids (arrow) in leaf trace as seen in C. A, B, USNM 446311; C, D, USNM 446312.





as *Monograptus* aff. *uncinatus uncinatus* Tullberg on the grounds that the preservation differs from any described post-Ludlow species and that the specimens are very close to European specimens of *M. uncinatus* sens. str. On the other hand, Jaeger (1978, 1979) claimed that certain morphological characteristics of *M. uncinatus* persist into the Devonian, and the morphology serves as a template for some evolutionary lineages of graptolites in the Devonian. Such an observation suggests that objectivity in the definition of a taxon is prerequisite to defining graptolite biozones (Temple, 1988) and subsequently for defining an age for a stratigraphic occurrence of a potentially significant taxon. If specimens of graptolites are abundant at both localities, as stated by Garratt & Rickards (1984), more effort should be applied to define taxa as support for the determination of the age of the occurrences.

The plant remains found at Garratt and Rickard's Localities 4 and 1 are referred to as the "Lower Plant Assemblage." The *Baragwanathia longifolia* found at Locality 4 is conspecific with fossil remains found in an "Upper Plant Assemblage," the fossil flora described by Lang & Cookson (1935), which is dated as Pragian in age (middle Lower Devonian) (Jaeger, 1966, 1967). The two assemblages are vertically separated by 1,700 m of sediment. If the Lower Plant Assemblage is of Gorstian age (lower Late Silurian) and the age of the Upper Plant Assemblage is Pragian (middle Lower Devonian), then the section of sediments was accumulated over a period of about 24 million years. During that period no significant change occurred in the composition of the floras or assemblages. It seems unusual that such assemblages of plants would remain so static, with no evolutionary changes, for such a long period of time. The occurrences of the remains of the plants indicates that they were dislodged and drifted from their sites of growth on a landmass bordered by marine waters. It is hazardous to attempt to interpret the paleo-latitude or paleo-longitude of their occurrences, if the sites are among any of those accretionary terranes that appear to form a large part

of the eastern quarter of the present-day continent of Australia (Condie, 1988, fig. 6.26).

Baragwanathia, as an example of an advanced form of an early land plant, is not the sole basis for our discussion over the differing ages assigned to the two assemblages. The discussion rests more logically on the occurrence and identical representation of three of the four major groups of early land plants in the two assemblages, i.e., Rhyniophytina (*Salopella*), Zosterophyllophytina (zosterophyll species), and Lycophytina (*Baragwanathia*) (Tims, 1980; Tims & Chambers, 1984; Holmes, 1988). The Trimerophytina, the fourth group, is represented only in the Upper Assemblage by *Dawsonites subarcuatus* Tims & Chambers. The three plant groups common to the assemblages are at the same level of evolutionary development, and yet it is proposed that they are separated in time by 24 million years. Fossil evidence for the evolution of a flora of the type comprising the Lower Plant Assemblage is lacking for the period of time between the *Cooksonia* sp. of Late Homeric age in Ireland (Edwards & Feehan, 1980) and the Lower Plant Assemblage here in question. That period of perhaps three million years would have been followed by a stasis in the evolution of the flora for 24 million years. If the two assemblages are treated as similar or identical associations in more nearly synchronous occurrences, then there is fossil evidence for their evolution based on numerous, similar, well-dated associations in widely geographically separated localities (Chaloner, 1970; Chaloner & Sheerin, 1979; Banks, 1980). The levels of evolutionary development of these associations are not based solely on the rhyniophytes but instead are interpreted on the basis of all of the component taxa. The early rhyniophytes (e.g., *Salopella* Edwards & Richardson, 1974) should no longer be considered the basis for deriving lineages of all land plant groups, but instead the possible progenitors of the lineage of the Trimerophytina. A plexus of cooksonioid plants may, on the other hand, represent the basis for the derivation of the lineages of the Zosterophyllophytina and the Lycophytina. In the early land floras (Late

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FIGURE 7. A, B, C. *Asteroxylon mackiei* Kidston & Lang, 1920.—A. Median, longitudinal section of a permineralized, small, lateral axis in which the apical meristem is well preserved.—B. Tracing of the photograph in A with arrows to indicate (1) transverse sections of young leaves, (2) zone of apical initials, (3) leaf primordia, (4) zone of central mother cells, (5) procambium of vein of leaf, (6) zone of differentiation of the zoned cortex, (7) zone of procambium with xylem differentiation, (8) leaf traces.—C. Enlarged view of the apical meristem in which details of cells in the zones noted in B can be more clearly observed.—D. *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland, 1948. Compression fossil of young lateral axis, which if permineralized would perhaps exhibit the same organization of the stem apex as in A-C. A-C, USNM 446313; D, USNM 446314.

Silurian and Earliest Devonian) the lineages were independent, and their evolution proceeded at a rapid rate during the late Lower Devonian, Middle Devonian, and into the Upper Devonian. The northern and southern early land floras, although disjunct as fossil remains in their present distributions, are essentially in synchronization and need not be modified by the advent of interpretations that are insufficiently well founded to be readily accepted.

The Pragian (middle Early Devonian) age of *Baragwanathia longifolia* and its associates (Jaeger, 1966, 1967; Tims & Chambers, 1984; Holmes, 1988), as opposed to Gorstian (Lower Ludlow), seems more realistic in light of the fossil evidence at hand and for the general scheme of evolution of the Kingdom Plantae.

The story of the early lycopsids and their subsequent evolution may begin with a very fine, unique, and perhaps ancient species: *Baragwanathia longifolia* has all of the defining features of a lycopsid, and approximately 25 million years after its putative first appearance in the fossil record it is followed or accompanied by an array of fossil plant remains that are interpretable as lycopsids. Some of these fossils may not belong to the lineage at all, because although they may exhibit morphologies characteristic of the lycopsids, fertile specimens are not available to confirm the identifications. It is beyond the scope of this paper to attempt a revision of all of the species of early lycopsids. Such a revisionary task would require a highly objective re-examination of all of the specimens used to derive a particular species concept. I am attempting, at this time, to relate my own experiences with the problems of defining the species of fossil lycopsids, lycopsidlike plants, and their associates. The lycopsids are common in nearly all deposits of Devonian plant remains. The herbaceous forms reached their maximum diversity in a ca. 29-million-year span of time between middle Early Devonian (Pragian) and early Late Devonian (Frasnian). Where and when the arborescent habit was derived from the large stock of Middle Devonian herbaceous lycopsids remains unclear.

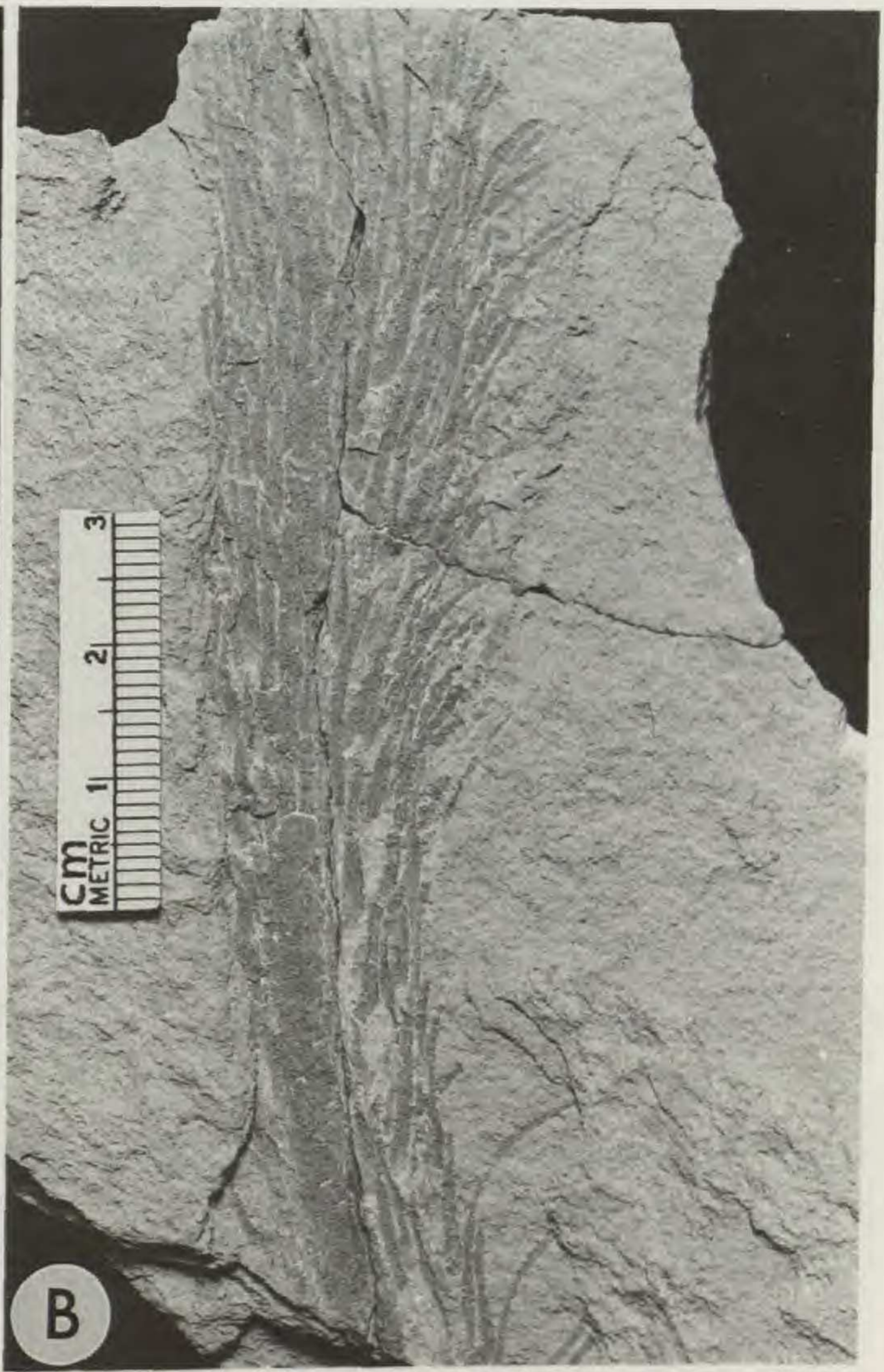
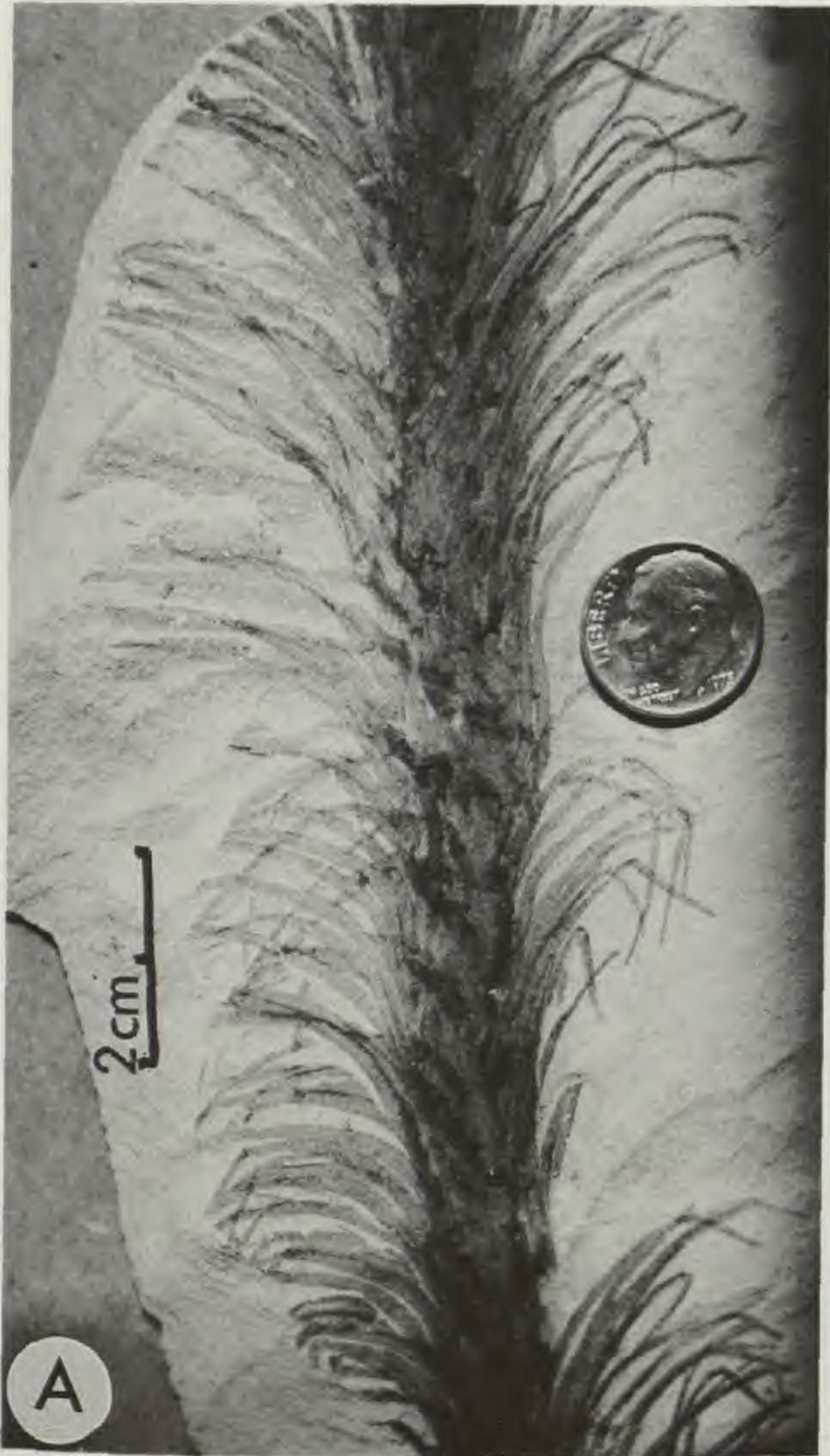
Baragwanathia longifolia can be recognized as a lycopsid (Fig. 8A–D, Fig. 9A–D; see also Lang & Cookson, 1935, plates 29–31), and its mor-

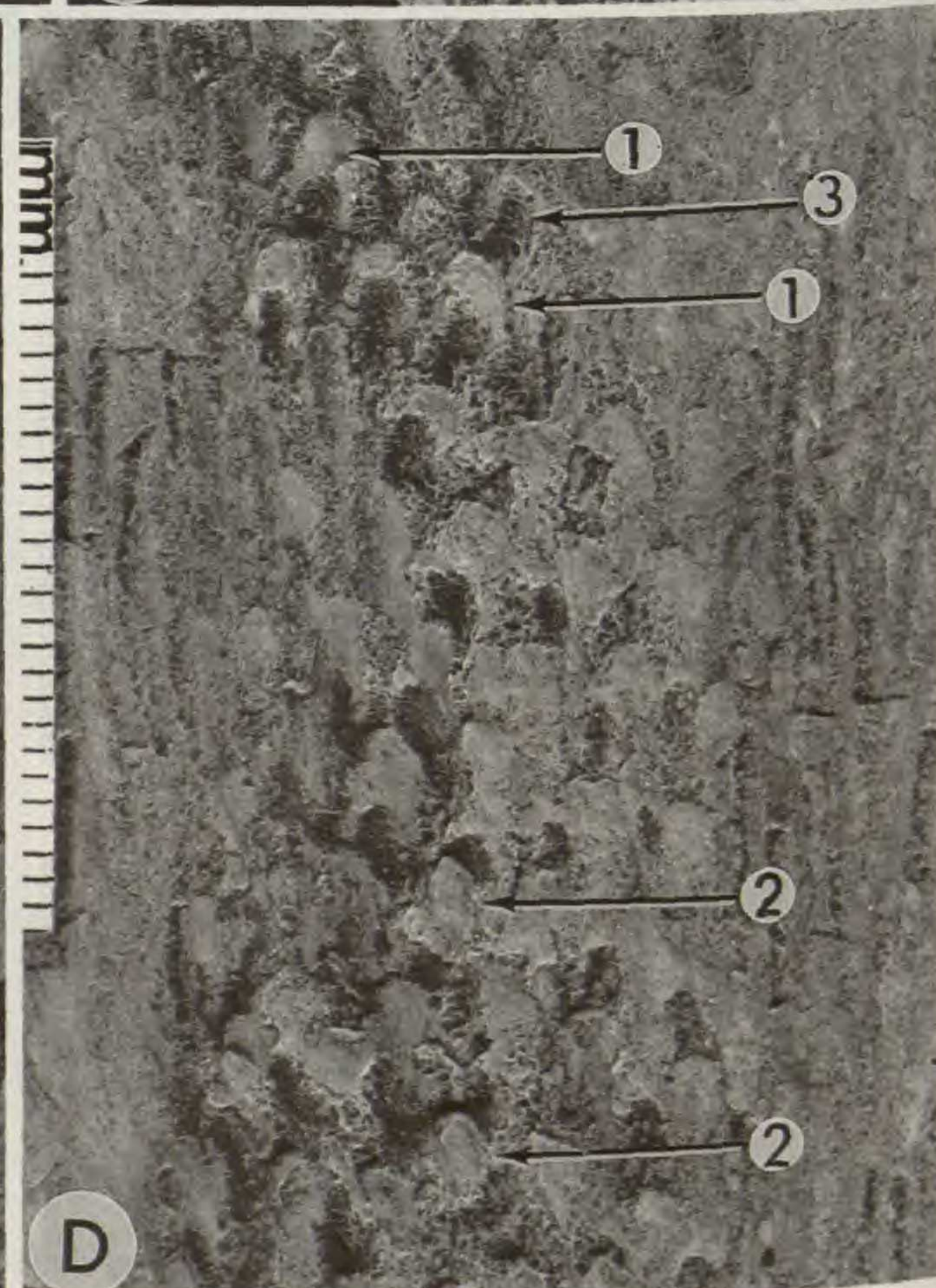
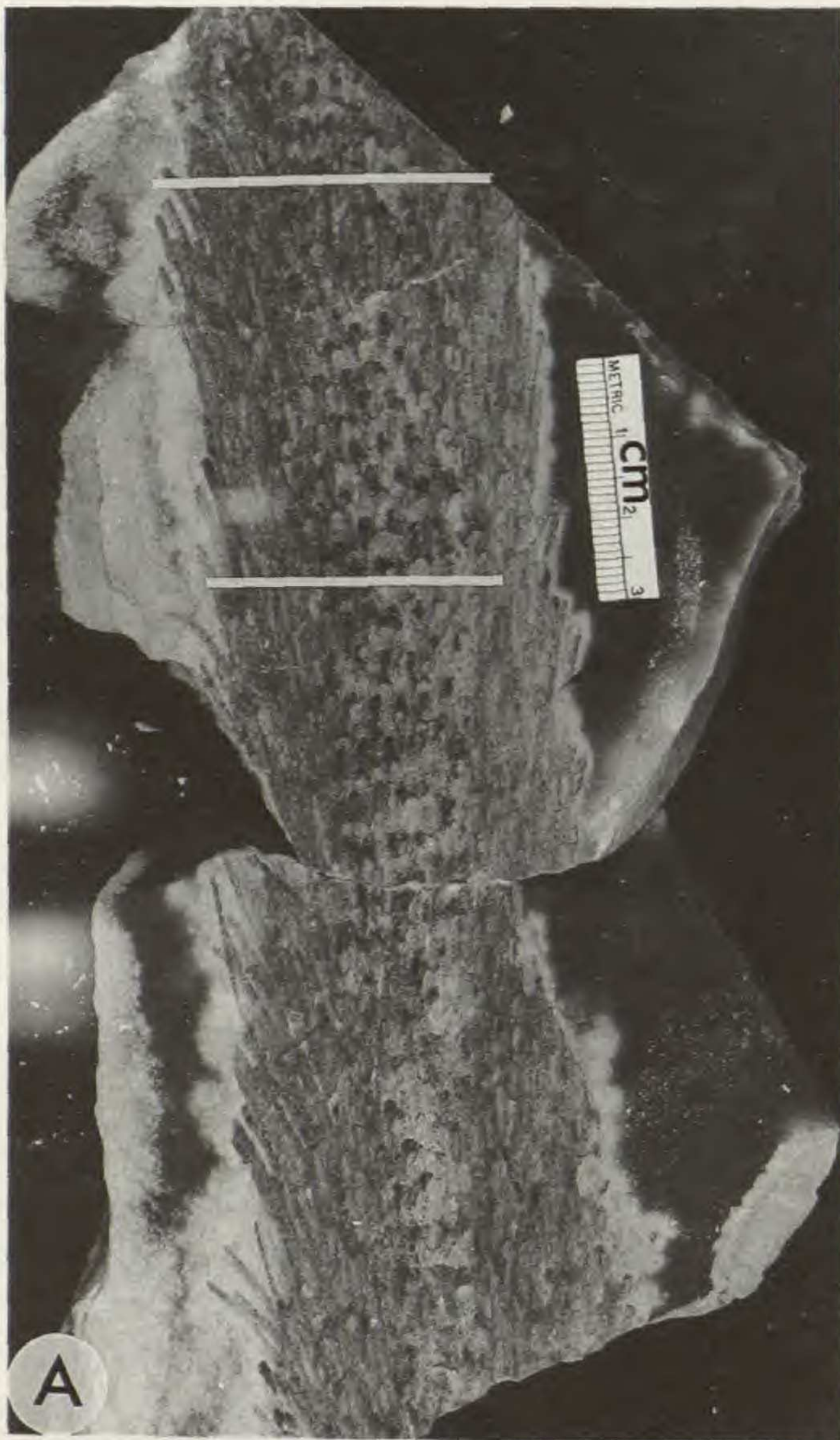
phology is homologous with that of some Recent species (e.g., *Lycopodium mandiocanum* Raddi; Fig. 10A, B). A morphologically comparable species, *B. abitibiensis* Hueber, 1983, occurs only slightly later in late Lower Devonian strata of Emsian age in northern Ontario, Canada. If the earliest date is correct, these occurrences establish a time span of approximately 35 million years during which *Baragwanathia* occupied its niche in the early land floras. The first appearance of *Baragwanathia* in the fossil record de novo, if it is correctly dated, is an enigma. Its extinction is a matter of conjecture, which will be discussed below.

Specimens of *Baragwanathia* bearing sporangia are uncommon. I collected a single specimen at the Nineteen Mile Quarry site in Victoria, Australia, and it is illustrated here in Figure 9A–D. Part and counterpart of the specimen are illustrated along with photographic enlargements of portions of the axis. The mode of preservation of the axis presents problems in interpretation of the morphology and position of the sporangia. A layer of microcrystalline quartz and an unidentified mineral containing barium was formed within the cavity that resulted from the decay of the fleshy, inner tissues of the plant. The minerals formed casts of the leaf bases and at the same time minutely dissected the carbonized remains of the sporangia. The mineralized layer split unevenly, resulting in irregular exposure of the upper and lower surfaces of the axis as it lies along the bedding plane of the matrix. In Figure 9C and 9D an attempt has been made to label the abaxial and adaxial view of the leaf bases and their associated sporangia, which appear to be axial in position. Because of the fragmentation of the sporangia, a line of dehiscence is difficult to recognize and illustrate; however, two examples are noted in the illustrations as slitlike, curved openings along the distal margin of the sporangia. Lang & Cookson (1935) demonstrated the presence of spores in the sporangia observed in their specimens. I have not yet had such good fortune. This information regarding the position and dehiscence of the sporangia is valuable in furthering the recognition of *Baragwanathia* as a lycopsid.

A description of *Baragwanathia longifolia* is here based on an analysis of the holotype and

FIGURE 8. A, B, C, D. *Baragwanathia oblongifolia* Lang & Cookson, 1935.—A. Vegetative axis from the Upper Plant Assemblage in the Devonian of Victoria, Australia; USNM 446315.—B. Vegetative axis from the Lower Plant Assemblage in the Silurian of Victoria, Australia; USNM 446316.—C, D. Part and counterpart of "pseudomonopodially" branched axis from the Upper Plant Assemblage in the Devonian of Victoria, Australia; USNM 446317.





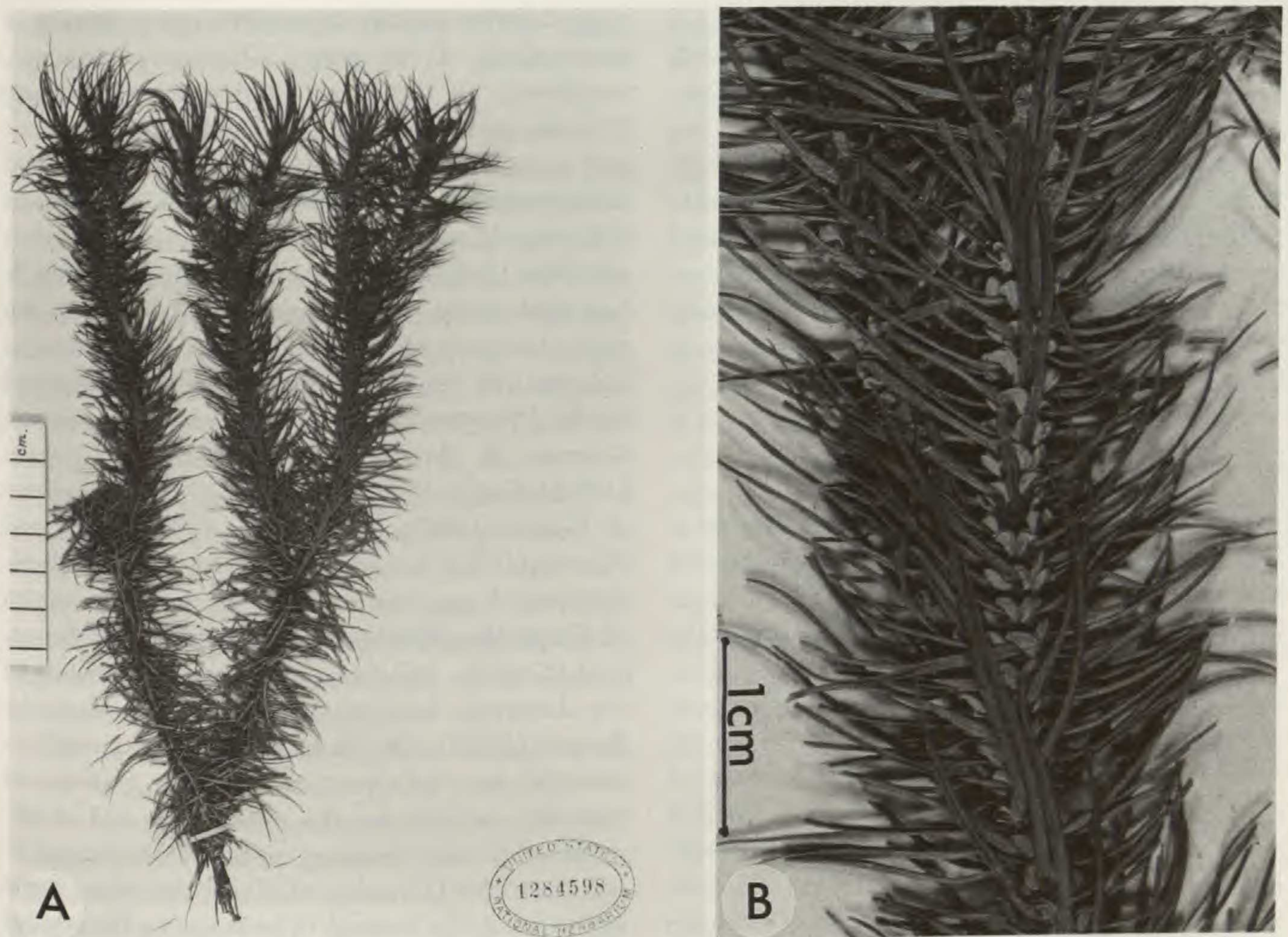


FIGURE 10. A, B. *Lycopodium mandioccanum* Raddi for comparison with *Baragwanathia longifolia*.—A. Specimen illustrating the morphology of the axis and leaves.—B. Enlarged view of the axis showing position and morphology of the sporangia.

paratypes in conjunction with a large suite of specimens housed in the Museum of Victoria in Melbourne, the collections of Jack Douglas, Melbourne, and small collections I obtained at the sites of the Lower Plant Assemblage and the Upper Plant Assemblage in Victoria, Australia. The sequence of details for characterization of the species coincides with that given in the list at the beginning of this paper. *Baragwanathia longifolia* is a vascular plant with stem, true roots (not rhizoids), and leaves; reproduction vegetative and by spores; terrestrial; recumbent; branching dichotomously to pseudomonopodially; fleshy herbaceous; roots adventitious; leaves microphyllous, entire, simple, arranged in helices; sporangia borne in axils of leaves, in fertile regions on the stem, dehiscence by distal

slit transverse to the leaf; homosporous; spores trilete; vascular strand protostelic, exarch, lobed; leaf traces ascend upwardly from margins of xylem strand as a single vein. Certain attributes of the species are based on interpretation of the fossils with regard to their occurrence, appearance, and state of preservation. The rarity of fertile specimens as compared with the abundance of vegetative material suggests that vegetative reproduction by fragmentation was a character of the species; this point will be discussed below in connection with other lycopoids. The presence of well-developed roots suggest that the plant was terrestrial, and there is no record of other plants of sufficient size on which it could be an epiphyte. Its recumbent habit is based on interpretation of the morphology of large

FIGURE 9. *Baragwanathia longifolia* Lang & Cookson, 1935.—A, B. Part and counterpart of fertile portion of axis.—C, D. Enlarged views of areas as marked in A, B and with arrows to define (1) adaxial view of a sporangium with cast of a leaf base in front with cast of a leaf base behind the sporangium, (2) abaxial view of a sporangium, and (3) partially displaced line of dehiscence along distal margin of sporangium. A, B, USNM 446318.

specimens. That the species was fleshy is discussed in a later section of this paper in connection with other fleshy members of the early lycopsid complex. The roots are adventitious, as they are seen in some specimens to arise directly from the leafy stems. The sporangia are defined as eusporangiate on the basis of extrapolation from the morphology and position of sporangia in Recent representatives of the group. The remaining characters are clearly observable in the suite of specimens available in the collections mentioned above.

DREPANOPHYCUS: ANOTHER EARLY LYCOPSID

From the advanced, early lycopsid *Baragwanathia* we retrogress to the less-advanced, somewhat less-organized genus *Drepanophycus*. At its earliest occurrence, in the Devonian, *Drepanophycus* is reported from the uppermost Lochkovian (Gedinian) at Vichtbachtal near Rötgen, Germany (Schweitzer, 1980). That occurrence is about 25 million years after the ostensibly first appearance of *Baragwanathia*. The two genera occur together at the latest occurrence of *Baragwanathia* in sediments of Emsian age (Hueber, 1983). *Drepanophycus* is last reported from sediments of Frasnian age by Banks & Grierson (1968) thus indicating that the genus existed for at least 22 million years. The type species of the genus, *D. spinaeformis*, may be characterized as follows: vascular plant with stem, true roots and leaves, reproduction vegetative and by spores; terrestrial; recumbent; branching dichotomously to pseudomonopodial; herbaceous; roots adventitious, branching dichotomously; leaves microphyllous, entire, simple, arranged in helices or randomly; "eusporangiate" sporangium borne on adaxial surface of normal leaf, or on short stalk with or without relationship to a leaf, in alternating fertile and sterile regions on the stem, dehiscence distally, transverse to the leaf or tangentially to the surface of the main axis; spores as yet not described; vascular strand protostelic, maturation exarch, variously lobed, traces to leaves extend upwardly from the ridges of the xylem entering the leaf as a single vein.

Which characteristics in the description of *D. spinaeformis* differ from those given for *Baragwanathia* and those in the broader characterization of the Recent lycopsids? First, the arrangement of the leaves in *Drepanophycus* can be random, which is not a characteristic of *Baragwanathia* but can be found in the Recent lycopsids. Certainly the lack of the character in *Baragwanathia* does not diminish its classification with the lycopsids even though, generally, the presence of helically ar-

ranged leaves usually is weighted more heavily in the analysis of the group. *Drepanophycus spinaeformis*, on the other hand, can possess both helically and randomly arranged leaves and can just as well fit into a broader concept of the leaf arrangement typifying the lycopsids. The second differing characteristic, and the one most used to eliminate *Drepanophycus* from the lycopsids, is how and where the sporangia were borne on the plant. I cannot add any evidence to this discussion because I do not have well-preserved specimens of fertile *Drepanophycus*. The reader may consult Grierson & Banks (1963), Banks & Grierson (1968), Fairon-Demaret (1971, 1978), Schweitzer & Giesen (1980), Schweitzer (1980, 1983) and Rayner (1984) for additional descriptions and discussions. A report on collections from the region of Gaspé Bay, Quebec, and northern New Brunswick, Canada, was given at the annual meeting of the American Institute of Biological Sciences by Kasper (1977). The illustrations used in conjunction with the oral report indicated the presence of valuable material for the description and clarification of details centering on fertile *Drepanophycus* from the Devonian of North America. Some of the sporangia seemed to be borne on the adaxial surfaces of leaves, but the careful preparation required for elucidating the details has not yet been completed.

As the reader might gather from my review of the sporangia of *Kaulangiophyton* and the speculations regarding the ontogeny of the sporangia in *Asteroxylon*, I am not convinced that the sporangia on *Drepanophycus* are borne on "stalks." I prefer to wait and see what is discovered with the preparations of better preserved specimens that lend themselves to maceration and isolation of the sporophylls for examination in three dimensions. The sporangia are of such large size, and as in *Kaulangiophyton*, they may exceed the length of the leaf and may mask its apex. Some of the drawings of the sporophylls of *Drepanophycus spinaeformis* by Kräusel & Weyland (1935) may be interpreted in that way and may serve as the basis for making closer observations of nearly prepared material. At the same time, there has been little attention given to the mode of dehiscence in *Drepanophycus*. In his description of specimens of *Drepanophycus (Protolycopodites) devonicus* (Weyland & Berendt), Schweitzer (1980) mentioned the presence of thickening along the upper margin of the sporangium, which he attributes to originating probably from the line of dehiscence. The detail is illustrated in the reconstruction of the sporangium, but is not clearly defined in the reconstruction of

the whole plant. The same is true of his reconstruction of the whole plant of *D. spinaeformis* (Schweitzer, 1980).

The line of dehiscence and its position on the sporangium among the early lycopoids offers little or no support for interpreting the phylogeny of the group. There are only two positions of the line of dehiscence known for the early lycopoids. The dehiscence of the sporangium distally and longitudinally to the axis of the leaf is, for example, characteristic of *Drepanophycus*, *Protolepidodendron* Kräusel & Weyland, 1932, *Colpodexylon*, *Leclercqia* Banks et al., 1972, and the later appearances in the Carboniferous of the arboreous and arborescent lepidodendrolean lycopoids and the ancestral stock of the Recent Isoetales. Dehiscence of the sporangium distally and transverse to the axis of the leaf is characteristic of *Baragwanathia*, *Asteroxylon* (probably) and most of the Recent members of the Lycopodiales.

The morphology of the xylem strands of the above examples reveals that lobed protosteles are characteristic of *Drepanophycus*, *Colpodexylon*, *Baragwanathia*, and *Asteroxylon*, while solid, coronate protosteles are characteristic of *Protolepidodendron* Stur, 1882, *Leclercqia*, and the Carboniferous lepidodendrolean lycopoids. Only in the characteristics of the xylem do I feel that some element of a phylogeny might possibly be derived. I have held this opinion and expressed it orally at the Tenth International Botanical Congress in Edinburgh (Hueber, 1964) after the publication of the details of the anatomy of *Protolepidodendron gilboense* Grierson & Banks, 1963, and before the publication of the details of the anatomy of *Drepanophycus gaspianus* (Grierson & Hueber, 1967). The lobed protostele of the early lycopoids may well be reflected in the variously lobed and dissected protosteles that characterize most of the Recent Lycopoida, whereas the solid, coronate protostele seems to have been the basic form on which the arboreous and arborescent, lepidodendrolean lycopoids expanded and then declined, leaving the Isoetales as the only Recent derivative to retain this particular trait.

MORPHOLOGY OF THE LEAVES OF EARLY LYCOPSIDS

The morphology of the leaves of the early lycopoids shows an even greater disparity among the genera. No clear phylogenetic signal can be derived from them. There are simple leaves in *Drepanophycus*, *Baragwanathia*, *Asteroxylon*, *Lycopodites oosensis* Kräusel & Weyland, 1937, and the Carboniferous lepidodendrolean lycopoids. *Proto-*

lepidodendron has bifurcate leaves. *Colpodexylon* has trifurcate leaves. *Leclercqia* has quinquefurcate leaves. There also are sagittate-entire leaves as in *Haskinsia colophylla* Grierson & Banks, 1983; hastate-entire leaves as in *H. sagittata* Edwards & Benedetto, 1985; deltoid-serrate leaves as in *Archaeosigillaria vanuxemii* (Göppert) Kidston, 1901 (Fairon-Demaret & Banks, 1978) and *Artschaliphyton unicum* Senkewich, 1971 (not seen; publication date pers. comm. H. P. Banks, species = *Gilboaphyton goldringiae* Arnold, 1937; Kräusel & Weyland, 1949; Senkewich, 1956); and linear-serrate leaves as in *Barsostrobus famennensis* Fairon-Demaret, 1977. Presented here in Figure 11A–R are illustrations of these various leaves. The information that these illustrations supply is of taxonomic value, though that is all that can be said with confidence.

Bonamo et al. (1988) pointed out the value of leaf morphology in the identification of genera in which the morphology of the surfaces of the stems otherwise appear identical. This observation is particularly true in the genera they discuss: *Leclercqia*, *Protolepidodendron*, and *Haskinsia*.

EARLY LYCOPSIDS: ANATOMY OF EXTINCTION

The species among the early lycopoids *Baragwanathia*, *Drepanophycus*, and *Asteroxylon* apparently were fleshy or at least did not have the hypodermal layers of thickened, fiberlike cells evident in the other contemporaneous lycopoids. The trabeculate, aerenchymalike tissue that appeared to form the major part of the cortex in *Asteroxylon* may be the model for the other "fleshy" genera. In most specimens of *Baragwanathia* and especially in *Drepanophycus*, all that remains in the compression fossils of the axes is the cuticle of the stem and leaves, the xylem strand, and the leaf traces. The xylem strand in compressions generally is about one-eighth to one-tenth the diameter of the stem. Such a strand could hardly have given much support to the axis. Observations (Kidston, 1893; Halle, 1916; Kräusel & Weyland, 1935; Rayner, 1984) have led to the interpretation that the axes and leaves were parenchymatous. The axes probably had either thick zones of cortical parenchyma or a combination of such parenchyma and aerenchymalike tissue comparable to that mentioned earlier as typical in the stems of *Asteroxylon*. Turgor pressure within the tissues of the stem could have maintained the ability of the stems to stand erect above the substrate. I do not interpret these stems as those of halophytes, as was expressed by Kräusel & Weyland (1935), nor did

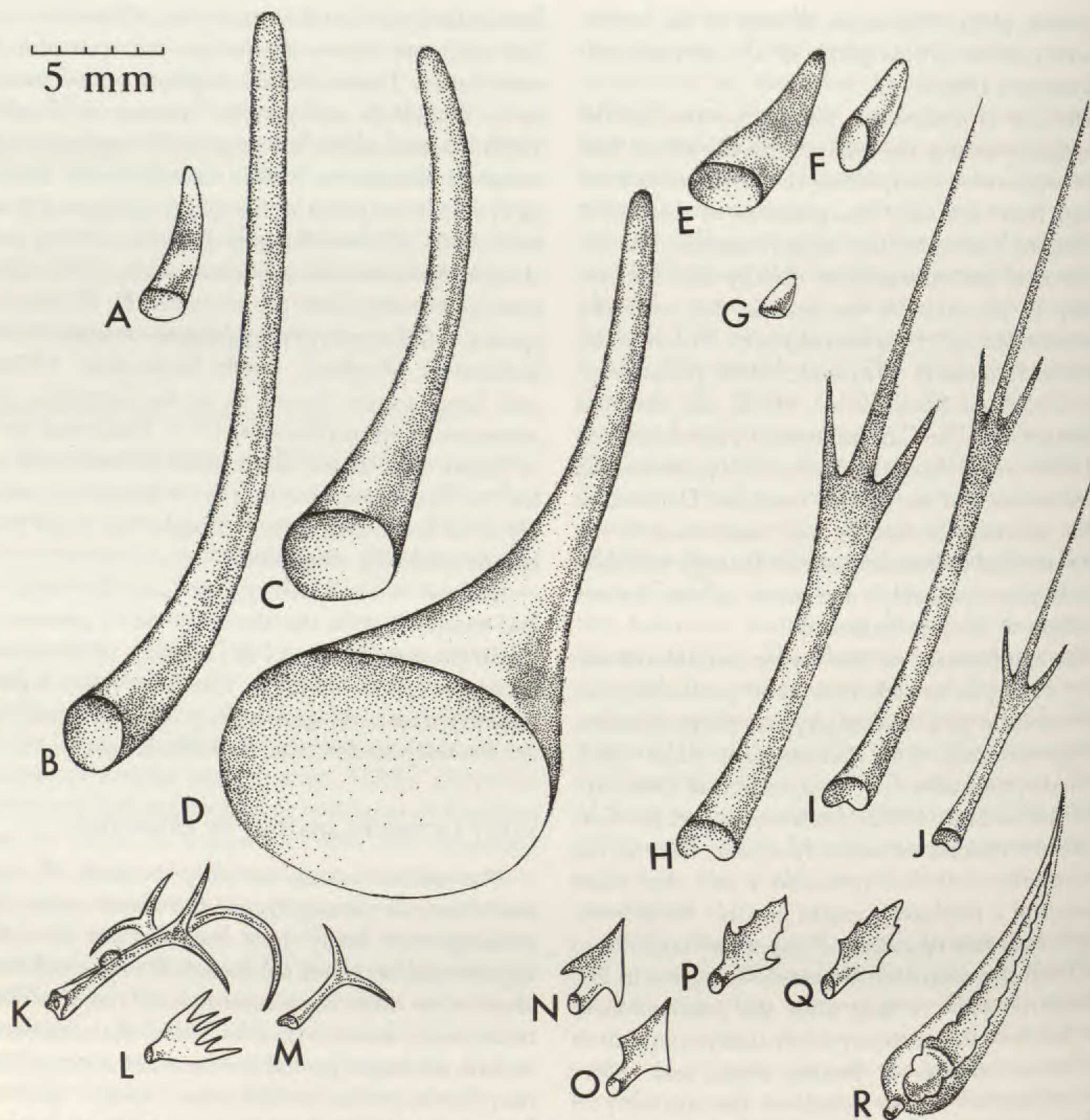


FIGURE 11. Generalized restorations of the morphology of the leaves of early lycopsids.—A. *Asteroxylon mackiei* Kidston, 1901.—B. *Baragwanathia longifolia* Lang & Cookson, 1935.—C. *Baragwanathia abitibiensis* Hueber, 1983.—D. *Drepanophycus spinaeformis* Göppert, 1852 (large form).—E. *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland, 1948.—F. *Drepanophycus spinaeformis* (Dawson) Kräusel & Weyland, 1948 (small form).—G. *Lycopodites oosensis* Kräusel & Weyland, 1935.—H. *Colpodexylon trifurcatum* Banks, 1944.—I. *Colpodexylon deatsii* Banks, 1944.—J. *Colpodexylon cachiriense* Edwards & Benedetto, 1985.—K. *Leclercqia complexa* Banks, Bonamo & Grierson, 1972.—L. *Leclercqia complexa* as identified by Kasper & Forbes, 1979.—M. *Protolepidodendron scharyanum* Stur, 1882.—N. *Haskinsia colophylla* Grierson & Banks, 1983.—O. *Haskinsia sagittata* Edwards & Benedetto, 1985.—P. *Archaeosigillaria vanuxemii* (Göppert) Kidston, 1901.—Q. *Artschalophyton unicum* Senkewich, 1971.—R. *Barsostrobus famennensis* Fairon-Demaret, 1977.

Halle (1916) interpret them in this manner. There is no evidence of association of the remains of the plants with the remains of marine or brackish water animals. The occurrences of *Drepanophycus* in Gaspé, Quebec and northern New Brunswick, Canada are in continentally derived freshwater sediments, and in many instances the plants occur in situ on or in mudstones suggesting that they preferred particularly wet sites. We have come full circle in an interpretation that the fleshy lycopsids

required turgor pressure within the axis to remain erect and therefore required an abundance of water as would have been available on mud flats or moist flood plains of rivers or lakes. It might be suggested also that the requirements for the successful development of the gametophytes of these early lycopsids were as highly specific as we see in the Recent lycopsids.

The extinction of the large (and very fleshy) early lycopsids may have been directly connected

with the relatively unstable habitats to which they had become adapted. Their growth was nearly completely vegetative with an attendant highly reduced reproduction by spores. Destructive floods would either partially or completely disrupt and carry away the colonies from their substrate or completely bury and obliterate the colonies under sediment. The few spores and even fewer gametophytes may have been the only, tenuous means by which new colonies could be reestablished under favorable growth conditions. With the continual breakup and disruption of the habitats of these early lycopoids and the concomitant changes in the availability of adequate water for their survival, it was likely that their numbers diminished rapidly, and any additional, major change of climate would have been the final factor in their extinction.

This scenario of extinction can be witnessed in a segment of the history of *Drepanophycus* in the extensive section of the Emsian into ?Early Eifelian sediments exposed around Gaspé Bay, Quebec, Canada (York River, Battery Point, and Malbaie Formations; McGregor, 1967). Along the north shore of the Bay, colony after colony of *Drepanophycus* is found buried in situ by coarse sediments of sufficient thickness to kill the colony. Interestingly, one finds in the coarser sediments fragments of *Drepanophycus* that had been brought from sites further upstream in the ancient river system. As one progresses upward in the section, the frequency of the genus diminishes. There are red beds of sediment indicating either drying of the surface of the delta or of the land mass from which the sediments were being derived. The genus is not found in the Malbaie Formation that comprises numerous redbeds and a spore flora indicating a displacement of the earlier flora represented in the preceding formations (McGregor, 1967).

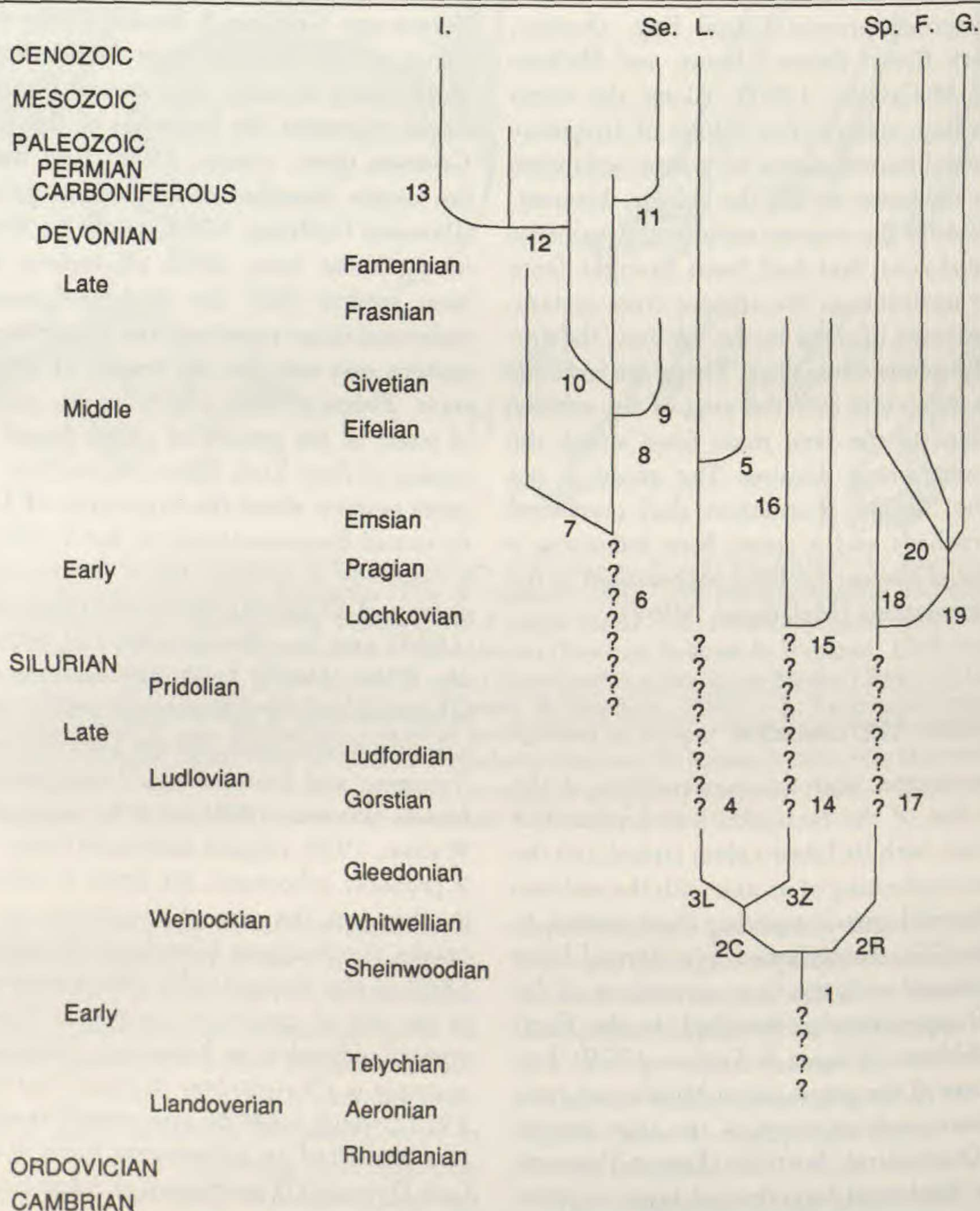
EARLY LYCOPSIDS: THE LINEAGES

We may suggest that the continuation of the herbaceous line of the lycopoids was a plant like *Colpodexylon*, with its lobed xylem strand and the structural strengthening of its axis with the addition of a hypodermal layer comprising thick-walled, fiberlike cells. This strengthened hypodermal layer perhaps appeared with the first occurrence of *Leclercquia*, if appropriately identified, in the Early Devonian of Maine (Kasper & Forbes, 1979). Later occurrences of the genus are in Middle and early Late Devonian such as those of the type species and that in Queensland, Australia (Fairon-Demaret, 1974). The thickened hypodermal layer is prominent in compressions as well as in permineraliza-

tions of the axes. The stems were probably considerably strengthened by the tissue, and the characteristic of the thickened hypodermis was carried through the Devonian and into the Carboniferous among the arboreous and arborescent lycopoids as well as into many species of Recent herbaceous lycopoids.

There is no evidence for a gradual advent of the arborescent habit among the early lycopoids. Instead, the arborescent forms appear de novo with the discovery of *Lepidosigillaria whitei* Kräusel & Weyland, 1949. It was found in marine black shales of early Late Devonian age (Frasnian) near Naples, New York, and became known as the "Naples Tree." The length of the trunk was not given, but it may have been as much as 10 m and was unbranched. The generic name was chosen to indicate that the trunk exhibited the form and arrangement of leaf cushions characteristic of the genera *Lepidodendron* and *Sigillaria* of Carboniferous age. Grierson & Banks (1963) thought that many of the lycopoid axes found in the marine black shales at many sites around New York State might represent the branches of the genus. J. D. Grierson (pers. comm. 1978) held the idea that the trunks identified as *Eospermatopteris textilis* (Dawson) Goldring, 1924, might be those of *Lepidosigillaria* from which all surface tissues had been eroded. Only the thickened strands of hypodermal tissue remained and in turn produced the pattern one sees on the trunks of *Eospermatopteris*. Fisher (1962-1963), in his reconstruction of some of the genera of plants found in the Devonian of New York State, implied that he had the same opinion about the synonymy of *Lepidosigillaria* and *Eospermatopteris*, but he did not express it explicitly in writing. For a description and synonymy of *Lepidosigillaria* see Grierson & Banks (1963) and for photographs and full description see White (1907). I will only mention some other arboreous and/or arborescent genera and not give a description of each. All are Late Devonian in age (Frasnian and Famennian). *Leptophloeum rhombicum* Dawson, 1862, and *L. australe* (McCoy) Walton, 1926, require additional study, the former is probably arboreous, the latter is arborescent on the basis of the size of fragments of stems and trunks. *Cyclostigma kiltorkense* Haughton, 1859-1860, is also deemed to be arborescent on the basis of the size of specimens recovered from Late Devonian sediments in Kiltorcan, Ireland. One last example is *Phytokneme rhodona* (Andrews et al., 1971), which could be interpreted as arboreous or as a branch of an arborescent form; it is from the Late Devonian (Famennian) of Adair County, Kentucky.

TABLE 2. A partial summary of the evolution of the Lycophytina and Zosterophyllophytina as well as the hypothetical derivatives from the Rhyniophytina. (1) Plexus of unornamented, dichotomous axes of probable land plants. (2) Differing ontogeny of sporangia; 2C, the terminal globular or reniform cooksonioids; 2R, the terminal fusiform rhyniophytoids. (3) Differing ontogeny of the sporangia; 3L, Lycophytina; 3Z, Zosterophyllophytina (see text). (4) Axes with dissected xylem strand; simple singly veined leaves; sporangia borne in close relationship to leaves; homosporous. (5) Dissected xylem strand; trifid leaves; sporangium borne on adaxial surface of leaf; herbaceous habit; homosporous. (6) Origin of coronate xylem strand and ligule uncertain. (7) Coronate xylem strand; ligulate, five-parted leaf; herbaceous; sporangium borne on adaxial surface of leaf; homosporous. (8) Coronate xylem strand; ligulate, simple leaves; homosporous. (9) Coronate xylem strand; bifid leaves; sporangia borne on adaxial surface of leaves; homosporous. (10) Coronate xylem strand; ligulate; arborescent habit; rhizomorph; simple single-veined leaves; sporangia borne in axils of leaves; homosporous. (11) Dissected xylem strand; ligulate, simple leaves; heterosporous; herbaceous; rhizomorph. (12) Coronate xylem strand; ligulate; arborescent habit; rhizomorph; heterosporous. (13) Coronate xylem strand; ligulate; heterosporous; herbaceous; rhizomorph. (14) Stems smooth or variously ornamented with spines or nonvascularized emergences; sporangia cooksonioid in ontogeny and morphology, depleting whole of meristem; exarch protostele generally bipolar. (15) Terminal or lateral fertile spike, determinate in growth. (16) Fertile axis indeterminate in growth. (17) Axes smooth; branching dichotomous; sporangia terminal and fusiform, depleting the apical meristem during ontogeny. (18) Plants of determinate growth resulting from depletion of all apical meristems in the production of terminal, fusiform sporangia, sporangia apparently indehiscent. (19) Sporangia fusiform, borne terminally on lateral shoots, dehiscent; branching generally pseudomonopodial; some secondary tissues developed. (20) Plexus of plants with anatomically diverse xylem strands and arrangements of lateral vegetative and fertile shoots; basis for interpretation of subsequent evolutionary lines; homosporous predominant; heterospory and seed-megaspores appear along with increased secondary growth. No attempt is made here to elucidate the evolution of plants outside of the lycopsids. I. = *Isoetes*; Se. = *Selaginella*; L. = Lycophytina; Sp. = Sphenopsida; P. = Pteropsida; G. = Gymnospermopsida.



We still lack sufficient data to propose or demonstrate any clear evolutionary pathways among the early lycopoids, and there is no evidence for pre-lycopoids (or "pro-lycopoids"), if *Baragwanathia longifolia* is accepted as the oldest representative of the lycopoid lineage. All attributes of that species were realized in the same length of time (Wenlockian-Gorstian) that was required for the zosterophylls to become recognizable in the early floras. The lycopoids were precocious in their production of leaves, which served as improved and more efficient organs for increased photosynthesis. The zosterophylls never seemed to derive the ability to produce anything more than an array of usually randomly arranged trichomes or emergences. The value of these outgrowths may have been for clambering on or around one another, much as one can see today in *Galium*, *Rubus*, or *Rosa*. Of course the outgrowths could also have served as protection against predation by arthropods and other early, terrestrial animals, which were evolving rapidly along with the plants.

My hypothesis as to the relationship of the zosterophylls to the lycopoids, as based on morphology and anatomy of the sporangium, is that they both perhaps had the same origin in a plexus of cooksonioid plants. However, the two groups became separate quite early, sometime between late Early Silurian and early Lower Devonian, perhaps on the basis of differing functions within the apical meristem for the production of sporangia. The zosterophylls utilized the whole of the apical initials in the production of a sporangium or parts of them to produce lateral axes that in turn utilized the whole of their apical initials in the production of sporangia. The lycopoids, on the other hand, utilized protodermal derivatives of the apical initials to produce leaves that were in turn the sites of the production of sporangia. The production of the leaf primordium was immediately followed by the production of the sporangial initials either from protoderm of the leaf or from cauline protoderm cells, which were derived immediately after those of the leaf primordium.

Perhaps all of these hypotheses will direct attention toward further, thorough investigation of the ancient lycopoids, which occur so abundantly and widely in the fossil record. We are fortunate to have a large and increasing number of techniques for preparation, study, and illustration of fossil plant remains, many of which were not available during the early history of paleobotanical study. With the determined use of the new techniques for study of specimens, some (though certainly not all) hypotheses may, in due time, be replaced by supportive evidence for description and interpretation.

In Table 2 a brief and partial summary is presented suggesting the evolution of the Lycophytina and Zosterophyllophytina, as well as the hypothetical derivatives of the Rhyniophytina.

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EXPERIMENTAL CLADISTIC
ANALYSIS OF
ANATOMICALLY PRESERVED
ARBORESCENT LYCOPSIDS
FROM THE CARBONIFEROUS
OF EURAMERICA: AN
ESSAY ON PALEOBOTANICAL
PHYLOGENETICS¹

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ABSTRACT

This evolutionary cladistic analysis of the arborescent (wood-producing) lycopsids, an exclusively fossil group of vascular plants, is confined to the strongest available data: anatomically preserved fossils that have been painstakingly reconstructed into conceptual whole plants. Ten Carboniferous genera are represented by 16 species: four pseudoherbs/"shrubs" and 12 of the arboreous (tree-sized) species that epitomize the Pennsylvanian coal swamps of Euramerica. The 69 vegetative and 46 reproductive characters are described in detail; several key terms are redefined and homologies reassessed. Binary coding was imposed throughout the data matrix, which contained only 5% missing values despite limited X-coding. Lack of an acceptable outgroup necessitated construction of a hypothetical ancestor for character polarization and tree rooting.

Our experimental approach analyzed the full data matrix plus four submatrices (growth habit characters excluded, *Chaloneria* excluded, vegetative characters only, reproductive characters only) and screened topologies of subminimal as well as minimal length. Interpretation focuses on the ten monophyletic genera and marginally favors the topology ((*Paurodendron*, *Oxroadia*) (*Anabathra* (*Chaloneria* (*Sigillaria* ((*Diaphorodendron*, *Synchysidendron*) (*Hizemodendron* (*Lepidodendron*, *Lepidophloios*)))))). Other parsimonious topologies allow dissociation of the *Paurodendron*-*Oxroadia* clade (probably justified), transposition or unification of *Anabathra* and *Chaloneria*, and addition of *Sigillaria* to the *Diaphorodendron*-*Synchysidendron* clade. The analysis confined to vegetative characters translocates *Hizemodendron* close to the base of the clade, thus uniting the non-trees as an ostensibly paraphyletic basal group. The analysis confined to reproductive characters more closely resembles the analysis of all characters, but fails to resolve relationships among the four basal, bisporangiate-coned genera, and between *Hizemodendron* and *Lepidodendron*. These observations cast doubt on the value of partial-plant and isolated-organ phylogenies.

Parsimonious use of the increasingly sophisticated and *K*-selected reproductive strategies as the basis of the overall phylogeny inevitably renders homoplastic the partly discordant vegetative architectures (including the tree habit). Consequently, a poorly resolved paraphyletic plexus of four primitive, bisporangiate-coned genera (*Paurodendron*, *Oxroadia*, *Anabathra*, *Chaloneria*) subtends a monophyletic monosporangiate-coned clade of three well-supported, monophyletic families: the Sigillariaceae (*Sigillaria*) are primitive relative to the Diaphorodendraceae (*Diaphorodendron* sens. str., *Synchysidendron*) and the Lepidodendraceae (*Hizemodendron*, *Lepidodendron* sens. str., *Lepidophloios*), which together are characterized by a single functional megaspore per megasporangium. This apparently progressive evolutionary trend toward seedlike reproduction increased ecological specialization and is consistent with adaptive scenarios.

In contrast with reproductive features, vegetative features such as the determinate growth, centralized rhizomorphic rootstock, and small number of module types that constitute the bauplan (rhizomorph and stem essential, lateral and crown branches optional) apparently predisposed the arborescent lycopsids to nonadaptive saltational evolution. Mutation of genes controlling early development allowed radical changes in growth architecture, and consequent

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epigenetic readjustment and adaptive honing affected many other vegetative characters. The progenetic (heterochronic) origin postulated for the pseudoherb *Hizemodendron* may also apply to *Chaloneria* and the other pseudoherbs (*Paurodendron*, *Oxroadia*), arguably comprising their value in scoring habit characters for the hypothetical ancestor.

Other limitations of the present data matrix are the large number of genus-level autapomorphies (at least partly reflecting the absence of pre-Pennsylvanian arboreal species), the inclusion of only one bisporangiate-coned tree (*Anabathra*) and of only one putative isoetalean (*Chaloneria*). More primitive OTUs are needed to investigate the origins of profound character states shared by all OTUs in the present study (e.g., secondary thickening, determinate growth, centralized rhizomorph, heterospory), and to confirm the crucial hypotheses of monophyly for the monosporangiate cone and the single functional megaspore. Repeated simplification of growth architecture by progenesis and of megaspore ornamentation by functional redundancy show that evolution did not consistently increase morphological complexity among the arborescent lycopsids. Synapomorphies of highest burden (and therefore lowest homoplasy) tend to represent features of intermediate scale.

We have not identified any significant drawbacks of cladistically analyzing an exclusively extinct set of OTUs. Rather, we recommend further study of some under-researched aspects of phylogeny reconstruction in general: (1) the effect of missing values on tree length calculations and on character state optimization; (2) the minimum acceptable level of empirical support (apomorphic states per OTU); (3) means of recognizing heterochrony in cladograms; and (4) less methodologically constrained phenetic adjuncts to strict cladistic analyses.

Coal-swamp floras from the Pennsylvanian of Euramerica have remained the most intensively investigated and best known of all Paleozoic plant communities throughout the last two centuries of detailed scientific study. Their popularity largely reflects the unusual abundance of spores, adpressed megafossils, and anatomically preserved megafossils in these depositional environments and the economic importance of coal (e.g., Scott, 1987). Studies of permineralized coal-ball floras (e.g., Scott & Rex, 1985) have been especially important in providing detailed information on the morphology and anatomy of the plants that comprised the coal-swamp communities (e.g., Taylor, 1981; Stewart, 1983; Bateman, 1991b; DiMichele et al., 1992). Early workers (e.g., Grand'Eury, 1877; Williamson, 1893; Scott, 1908; Seward, 1910) soon recognized that the majority of the coal-ball floras were of low diversity and dominated (both in terms of body size and biomass) by trees that exhibited clear morphological (and, by inference, phylogenetic) similarities to an extant group of ecologically insignificant, exclusively herbaceous, free-sporing plants, the lycopsids or "clubmosses" (see Appendix 1A for discussion of the nomenclature and systematics of higher taxa).

The fossil tree-lycopsids occur in a severely disarticulated condition, and must be painstakingly reconstructed if they are to be understood as biological entities. Some early speculative restorations of these plants were remarkably accurate (e.g., Grand'Eury, 1877). Recently, more rigorous reconstructions (DiMichele, 1979a, b, 1980, 1981, 1983, 1985; DiMichele & Phillips, 1985) have been achieved using evidence of organic connection supported by quantified association/dissociation values (e.g., Bateman & Rothwell, 1990) and par-

alleled by increased knowledge of ontogeny (Walton, 1935; Eggert, 1961; Chaloner & Meyer-Berthaud, 1983; Phillips & DiMichele, 1992) and reproductive biology (e.g., Thomas, 1978, 1981; Phillips, 1979).

Earlier higher classifications of the arborescent lycopsids focused on ostensibly well-known genera such as *Sigillaria*, *Bothrodendron*, *Lepidophloios*, and '*Lepidodendron*' sens. lat. and remained fairly stable throughout much of this century (see Chaloner, 1967, for the most detailed account). More recently, these conventional supraspecific classifications have been challenged. Thomas & Brack-Hanes (1984) devised a controversial system of satellite taxa that more accurately reflects the variable and fragmentary nature of the paleobotanical data, albeit at the expense of emphasizing reproductive structures rather than whole plants. Using a contrasting philosophy (but generating an equally controversial result), DiMichele (1979a, b, 1980, 1981, 1983, 1985) revised several arborescent lycopside genera as part of a program of whole-plant reconstruction, implicitly intended to delimit potentially monophyletic taxa within *Lepidodendron* sens. lat. This revision has been extended by Bateman & DiMichele (1991) and DiMichele & Bateman (1992).

We believe that sufficient credible whole-plant reconstructions of arborescent lycopsids are now available (Figs. 1, 2) to allow explicit phylogenetic analysis, using cladistic methods. To date, cladistic analysis has been applied sparingly to long-extinct (i.e., paleobotanical) species, which have invariably been admixed with their extant putative descendants. Most of these studies focused on seed plants (Hill & Crane, 1982; Crane, 1985a, b; Doyle & Donoghue, 1986a, b, 1987a, b; Donoghue & Doyle,